Current Natural Sciences

Qing-Hua WANG and Yu JIA

A Monograph of the Genus *Ulota* s.l. (Orthotrichaceae, Moss)

SCIENCE PRESS

edp sciences

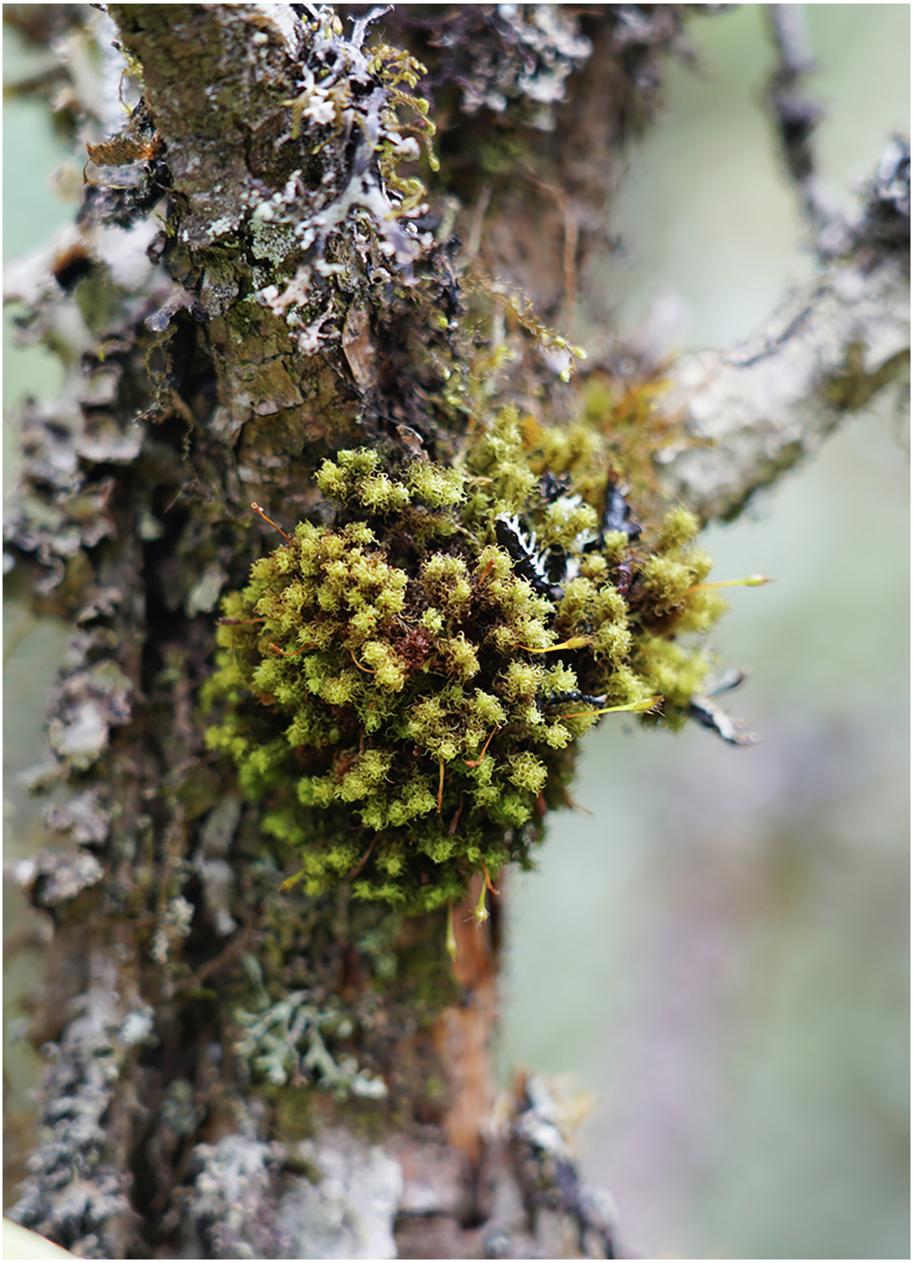
Printed in France

EDP Sciences – ISBN(print): 978-2-7598-2911-8 – ISBN(ebook): 978-2-7598-2912-5
DOI: 10.1051/978-2-7598-2911-8

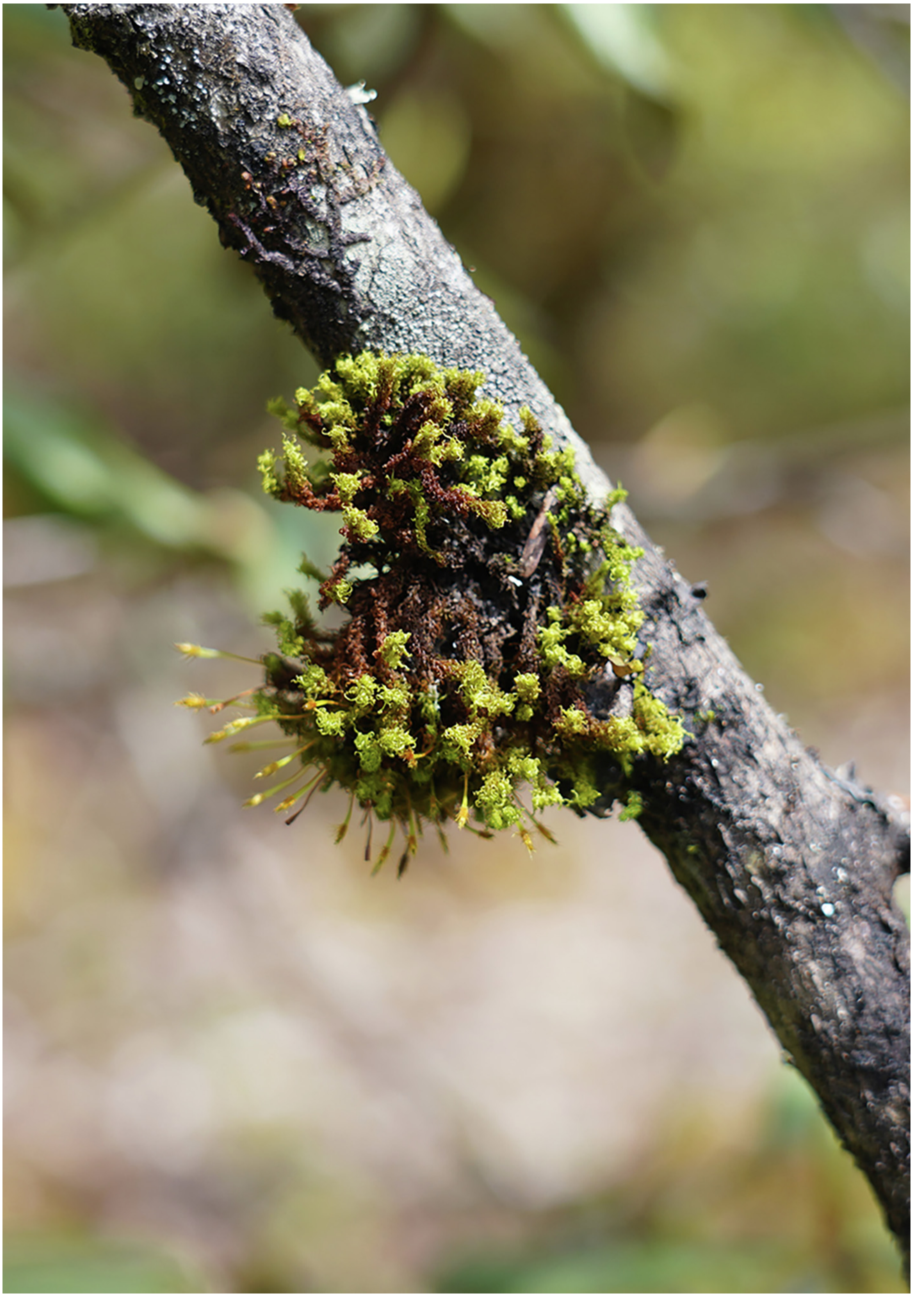
All rights relative to translation, adaptation and reproduction by any means whatsoever are reserved, worldwide. In accordance with the terms of paragraphs 2 and 3 of Article 41 of the French Act dated March 11, 1957, “copies or reproductions reserved strictly for private use and not intended for collective use” and, on the other hand, analyses and short quotations for example or illustrative purposes, are allowed. Otherwise, “any representation or reproduction – whether in full or in part – without the consent of the author or of his successors or assigns, is unlawful” (Article 40, paragraph 1). Any representation or reproduction, by any means whatsoever, will therefore be deemed an infringement of copyright punishable under Articles 425 and following of the French Penal Code.

The printed edition is not for sale in Chinese mainland.

© Science Press, EDP Sciences, 2023



Collection information: Sichuan Prov., Luding Co., alt 2584 m, *Q.-H. Wang 2578*, 2021.4.16.
Photographer: Qing-Hua Wang
Species information: *Ulota crispa* (Hedw.) Brid.



Collection information: Sichuan Prov., Luding Co., alt 2584 m, *Q.-H. Wang 2557*, 2021.4.16.
Photographer: Qing-Hua Wang
Species information: *Ulota intermedia* Schimp.

Contents

CHAPTER 1

Introduction 1

CHAPTER 2

Taxonomic History 3

2.1 Circumscription for the Genus 3

2.2 Discovery History of Species 4

2.3 History of Each Continent 4

CHAPTER 3

Material and Methods 11

CHAPTER 4

Taxonomy 13

4.1 Morphology 13

4.2 Taxa 32

  4.2.1 Recognized Species 35

    1. *Ulota angusti-limbata* E.B. Bartram 42
    2. *Ulota barclayi* Mitt 47
    3. *Ulota billbuckii* Garilleti, Mazimpaka & F. Lara 50
    4. *Ulota bruchii* Hornsch. ex Brid 53
    5. *Ulota calvescens* Wilson 57
    6. *Ulota coarctata* (P. Beauv.) Hammar 61
    7. *Ulota cochleata* Venturi 67
    8. *Ulota crispa* (Hedw.) Brid 71
    9. *Ulota crispula* Bruch ex Brid. 86
    10. *Ulota curvifolia* (Wahlenb.) Lilj 92
    11. *Ulota delicata* Q.H. Wang & Y. Jia 99
    12. *Ulota drummondii* (Hook. & Grev.) Brid 103
    13. *Ulota ecklonii* (Hornsch.) A. Jaeger 109
    14. *Ulota eurystoma* Nog 112

15. *Ulota fuegiana* Mitt . . . 117
16. *Ulota germana* (Mont.) Mitt . . . 126
17. *Ulota gigantospora* F. Lara, Caparrós & Garilleti . . . 130
18. *Ulota gymnostoma* S.-L. Guo, Enroth & Virtanen . . . 135
19. *Ulota hutchinsiae* (Sm.) Hammar . . . 138
20. *Ulota intermedia* Schimp . . . 145
21. *Ulota japonica* (Sull. & Lesq.) Mitt . . . 149
22. *Ulota larrainii* Garilleti, Mazimpaka & F. Lara . . . 154
23. *Ulota laticiliata* Malta . . . 155
24. *Ulota latisegmenta* Q.H. Wang & Y. Jia . . . 159
25. *Ulota luteola* (Hook. f. & Wilson) Wijk & Margad . . . 162
26. *Ulota macrocalycina* Mitt . . . 169
27. *Ulota macrodontia* Dixon & Malta . . . 174
28. *Ulota magellanica* (Mont.) A. Jaeger . . . 178
29. *Ulota maltiana* Garilleti & F. Lara . . . 182
30. *Ulota megalospora* Venturi . . . 186
31. *Ulota membranata* Malta . . . 191
32. *Ulota morrisonensis* Horik. & Nog . . . 195
33. *Ulota novo-guinensis* E.B. Bartram . . . 199
34. *Ulota obtusiuscula* Müll. Hal. & Kindb . . . 204
35. *Ulota panchengiana* Q.H. Wang & Y. Jia . . . 209
36. *Ulota perbreviseta* Dixon & Sakurai . . . 213
37. *Ulota perichaetialis* (Sainsbury) Goffinet . . . 217
38. *Ulota phyllantha* Brid . . . 221
39. *Ulota pusilla* Malta . . . 229
40. *Ulota pycnophylla* Dusén ex Malta . . . 233
41. *Ulota rehmannii* Jur . . . 235
42. *Ulota reptans* Mitt . . . 240
43. *Ulota rhytiore* (B.H. Allen) F. Lara *et al.* . . . 245
44. *Ulota robusta* Mitt . . . 247
45. *Ulota rubella* E.B. Bartram . . . 252
46. *Ulota splendida* E.B. Bartram . . . 257
47. *Ulota streptodon* Garilleti, Mazimpaka & F. Lara . . . 262
48. *Ulota viridis* Venturi . . . 265
49. *Ulota yakushimensis* Z. Iwats . . . 269
50. *Ulota yunnanensis* F. Lara, Caparrós & Garilleti . . . 274
4.2.2 Doubtful Species . . . 278
1. *Ulota orientalis* Fedosov & Ignatova . . . 278
2. *Ulota pacifica* Fedosov & Ignatova . . . 279
3. *Ulota phyllanthoides* (Müll. Hal.) Kindb . . . 279
4. *Ulota schmidii* (Müll. Hal.) Mitt . . . 280
5. *Ulota ventricosa* (Müll. Hal.) Malta . . . 280

CHAPTER 5

Result and Discussion . . . 283
5.1 Taxonomy . . . 283
5.2 Habitats . . . 283
5.3 Geographic Distribution . . . 285
5.4 Phylogeny and Evolution . . . 287

Acknowledgements . . . 291
Literature Cited . . . 293
Index to Scientific Names . . . 301
Appendix. List of All Legal Names in Genus *Ulota* . . . 305

Chapter 1

Introduction

We have revised the worldwide taxonomy of *Ulota* since 2006. It has been done for 16 years, and six papers have been published until now (Wang and Jia, 2018a,b, 2016, 2014, 2012a,b). We here make a comprehensive summary of the taxonomic study of *Ulota* in these years. The genus *Ulota* mentioned in this book is sensu lato unless otherwise noted. Because recent studies (Draper *et al.*, 2021; Plášek *et al.*, 2015) have separated some species into new genera based on molecular evidences including *Ulota phyllantha* Brid. (= *Plenogemma phyllantha* (Brid.) Sawicki, Plášek & Ochyra) and *U. calvescens* Wilson (=*Atlantichella calvescens* (Carrington) F. Lara, Garilleti & Draper).

Ulota is a complex and large genus composing about 60 species worldwide at the beginning of this study. It may be found in epiphytic, rarely saxicolous habitats, mainly in temperate areas, with few taxa extending into the tropics or subantarctic/subarctic regions (Albertos *et al.*, 2008; Vitt, 2003; Seppelt, 1978). Species identification in *Ulota* has been difficult for a long time. About half of the species, mainly from South America, have no further study since the original publication before our work (2012a, 2016). Additionally, the morphological difference between *Ulota* and *Orthotrichum* has been obscure, and the latter was revised by Lewinsky (1993) and Vitt (2014, 2003, 1971, 1970). A taxonomic revision of the genus *Ulota* can help clarify the differences between the two genera. Moreover, most previous studies on *Ulota* are regional catalogues, floras or revisions, and scattered new species contained. This is not only easy to cause repeated publication but also not conducive to deeply understand the range of morphological variation for those species widely distributed around the world. Finally, some areas need to be completely investigated, such as China, for which no comprehensive study of *Ulota* has been done before. Therefore, a worldwide taxonomic revision of *Ulota* is necessary and timely.

DOI: 10.1051/978-2-7598-2911-8.c001
© Science Press, EDP Sciences, 2023

Chapter 2

Taxonomic History

2.1 Circumscription for the Genus

The name *Ulota* was first proposed in 1806 by Mohr. At that time, he emphasized the importance of split at the base of calyptra because *Orthotrichum anomalum* Hedw. and *O. striatum* Hedw. have “calyptra carinato-canaliculato, carinis basi fissa”, while “calyptra sulcato-dorsato, sulcis basi subpartita” in *O. crispum* Hedw. Additionally, considering the crisped leaves in *Orthotrichum crispum*, Mohr separated a new genus from *Orthotrichum* with hesitation, *i.e.*, *Ulota*. But he did not list the species names of this new genus.

Not all other bryologists agreed with Mohr’s treatment. Hooker and Greville (1824) indicated, “Indeed, a more entirely natural and beautiful genus than that of *Orthotrichum*, as it at present stands, can scarcely be found in the whole department of muscology.” The *Orthotrichum* they mentioned at that time was still a large assemblage, including *Ulota*, *Schlotheimia* Brid. and *Groutiella* Steere. In 1869, Mitten put *Ulota* only as a section of *Orthotrichum*. In 1897, *Ulota* was still not accepted by Kindberg as a separate genus. Even in 1933, Malta stated that “in reality the separation of these two as distinct genera is based more on practical considerations than on differences in characters, and therefore it seems that *Ulota* can claim no higher rank than that of a subgenus of *Orthotrichum*.” The latin name of this new genus was once named *Weissia* (Lindberg, 1879), but it was abandoned later due to illegality.

Although there was much doubt about the circumscription of *Ulota* at first, it has been accepted by modern bryologists. The genus *Ulota* is gametophytically distinguished from *Orthotrichum* by the often crisped leaves when dry, which are usually erect in the latter. Moreover, there are several rows of hyaline cells at the leaf base in most *Ulota* species. Sporophytically, capsules in *Ulota* are almost always exserted and with superficial stomata. Using these characters, we can easily discriminate *Ulota* from *Orthotrichum* in most cases.

DOI: 10.1051/978-2-7598-2911-8.c002
© Science Press, EDP Sciences, 2023

2.2 Discovery History of Species

It has been more than two hundred years since the establishment of the genus *Ulota*, and about 180 names have been put into this genus, of which approximately 60 are still recognized by now (Wang and Jia, 2018b). Like the long history of the genus, most species names in *Ulota* were also firstly proposed long time before. Among them, 105 names were published in the 19th century, and 168 names before 1960. Many authors of these names appeared in previous regional studies, and we list some who have significant contributions.

First, Samuel Elisée Bridel–Brideri was one of the earliest authors who report new species of *Ulota*. In 1819, 1826, and 1827, he published ten new names, which included one variety and four new combinations. Of these names, three have been treated as synonyms, and two have yet to be recognized now. William Mitten, a British bryologist, described 23 new species of *Ulota* in his five papers from 1859 to 1891. These species were found all over the world, including Australia, Japan, North America, South America, New Zealand, and Portugal. At present, eight of them have been reduced into synonyms, eight are still doubtful, and the remainings are considered "good species". Nils Conrad Kindberg, a contemporary bryologist from Sweden, published 12 new species of *Ulota* from North America in his four papers from 1888 to 1892 (1888, 1889, 1891, and 1892 with Macoun). Today, only two are recognized, six have been synonymised, and four are still in doubt. Additionally, a bryologist in Switzerland, August Jaeger, transferred 11 species to *Ulota* in only two papers (1874 & 1880 with Sauerbeck), of which only two are confirmed by us. Another Latvian bryologist, Nicolajs Malta, revised the genus *Ulota* from South America and Australasia in 1927 and 1933, respectively. He described 19 new species, including three new combinations, seven new varieties, and one new subspecies. To date, five of them are recognized, six fell into synonymy, and others are in doubt.

In the last half-century, new species of *Ulota* were not found as many as before, but there are still some. Vitt (1993) described four endemic species in the flora of Papua New Guinea. Guo *et al.*, (2004) reported a new species from China. Recently, several Spanish bryologists (Garilleti *et al.*, 2015, 2012; Caparrós *et al.*, 2011) successively found five new species from China and Chile. Soon, Fedosov and Ignatova (2018) added two new species from Russia. In the process of *Ulota* revision, we have contributed three new species, all from China (Wang and Jia, 2018b, 2012a).

2.3 History of Each Continent

Asia:

The first records of *Ulota* from Asia were *U. robusta* Mitt. and *U. schmidii* (Müll. Hal.) Mitt. recorded by Mitten (1859) based on collections from India. Subsequently, he (1891) also described two new species from Japan, *i.e.*, *Ulota japonica* (Sull. & Lesq.) Mitt. and *U. reptans* Mitt. Soon, a new species and two other new records were added in Japan (Paris, 1906; Bescherelle, 1893), *i.e.*, *Ulota nipponensis* Besch., *U. crispula* Bruch and *U. drummondii* (Hook. & Grev.) Brid., as well as a new species was first described from China (Bescherelle, 1892), *U. bellissima* Besch. Since then, the discovery of new species (Caparros *et al.*, 2011; Guo *et al.*, 2004; Iwatsuki, 1969, 1959; Noguchi, 1939, 1937; Sakurai, 1935; Brotherus, 1929) and new records (Suzuki and Iwatsuki, 2011; Ignatov and Ochyra, 1994; Bardunov, 1974; Sakurai, 1935; Keller, 1914) has continuously increased the diversity of *Ulota* in Asia, with the reduction of a few species, including *U. longifolia* Dixon & Sakurai (Noguchi and Iwatsuki, 1989), *U. nipponensis* Besch. (Iwatsuki, 1991), *U. macrocarpa* Broth. (Guo *et al.*, 2007b), *U. bellissima* (Guo *et al.*, 2010). Recently, a critical revision of *Ulota* across all of Asia was made by us (2012a) in which 18 species were confirmed, including two new species, *U. delicata* Q.H. Wang & Y. Jia and *U. latisegmenta* Q.H. Wang & Y. Jia, and a name was reduced into synonym, *i.e.*, *U. hattorii* Iwatsuki. Soon, *Ulota intermedia* Schimp. (Fedosov and Ignatova, 2018), *U. megalospora* Venturi was newly reported from Asia (Suzuki and Iwatsuki, 2013), *U. longifolia* was rescruited (Suzuki and Iwatsuki, 2013), and *U. orientalis* Fedosov & Ignatova, *U. pacifica* Fedosov & Ignatova and *U. panchengiana* Q.H. Wang & Y. Jia have been described from Russia and China (Fedosov and Ignatova, 2018; Wang and Jia, 2018b), that ultimately resulting in 25 species reported from Asia.

Although the revision of *Ulota* in Asia has been published (Wang and Jia, 2012a), the study among regions is still very unbalanced. *Ulota* species in some region has been revised (Eastern India (Gangulee, 1976), Altai Mountain (Ignatov and Ochyra, 1994), Hunan Province (of China) (Guo *et al.*, 2007b), Israel (Heyn and Herrnstadt, 2004), Turkey (Lara *et al.*, 2010), and Russia (Fedosov and Ignatova, 2018)), even more than once (Japan: Suzuki and Iwatsuki, 2013; Noguchi and Iwatsuki, 1989; Iwatsuki, 1959). But *Ulota* in central, southern, and most western Asia remain poorly investigated, with only checklists or new records available (Ghahreman *et al.*, 2007).

In China, Bescherelle (1892) reported the first *Ulota* species: *U. bellissima* (= *U. robusta*). Later, Brotherus (1929) described *Ulota macrocarpa* (= *U. crispa* (Hedw.) Brid.) found in Hunan and Sichuan. *Ulota morrisonensis* Horik. & Nog. was founded in Taiwan in 1937. The first record of *Ulota crispa* in China was also from Taiwan (Nakanishi, 1963). In the next many years, Chinese bryologists contributed some new records (Guo *et al.*, 2010, 2007a; Mamtimin *et al.*, 2004; Gao, 1977) and new species (Guo *et al.*, 2004) of *Ulota*. Soon afterwards, *Ulota gigantospora* F. Lara, Caparrós & Garilleti and *U. yunnanensis* F. Lara, Caparrós & Garilleti, were described as new species from Yunnan (Caparros *et al.*, 2011). Recently, a taxonomic revision of Asian *Ulota* made new additions and exclusions (Wang and Jia, 2012a). This revision included two new species (*Ulota delicata* and *U. latisegmenta*), two new records of *U. rehmannii* Jur. and *U. yakushimensis* Z. Iwats., and two exclusions from the Chinese moss flora (*U. eurystoma* Nog. and *U. reptans*). Recently, Wang and Jia, (2018b) again described a new species from China, *i.e. Ulota panchengiana.* In this context, 13 species of *Ulota* have been recognized in China to date.

Oceania:

Oceania mainly comprises Australia, New Zealand, Papua New Guinea, and some neighbouring small islands. It is also made up of three island regions: Australasia, Melanesia, and Polynesia.

The earliest reports of *Ulota* species from Oceania were all from Tasmania, including *U. lutea* (Mitt.) Mitt. (as *Orthotrichum luteum* Mitt.), *U. cochleata* Venturi, *U. viridis* Venturi, *U. anceps* Venturi, and *U. weymouthii* Venturi (Brotherus, 1893; Weymouth, 1893; Hooker and Wilson, 1860; Mitten, 1859), and the latter two species were reduced as synonyms later (Wijk *et al.*, 1969). Rodway (1912) added a new record of *Ulota fulva* Brid. from Tasmania. When Malta (1933) revised the Australasia species of *Ulota*, he described five new species, *i.e.*, *U. bellii* Malta, *U. breviseta* Malta, *U. dixonii* Malta, *U. laticiliata* Malta, and *U. membranata* Malta. Subsequently, Bartram (1945, 1942) found three new species from Papua New Guinea, including *Ulota angusti-limbata* E.B. Bartram, *U. rubella* E.B. Bartram, and *U. splendida* E.B. Bartram. Meanwhile, Sainsbury (1945) further described a new species from New Zealand, *i.e.*, *Bryodixonia perichaetialis* Sainsbury, which was transferred to *Ulota* based on molecular evidence (Goffinet and Vitt, 1998). Then, Sainsbury (1955) added a new species (*Ulota novae-seelandiae* Sainsbury) and two new records (*U. pygmaeothecia* (Müll. Hal.) Kindb. & *U. rufula* (Mitt.) A. Jaeger) during the investigation of *Ulota* in New Zealand. Later, few new species and records from Oceania have published again, only include the new species of *Ulota novo-guinensis* E.B. Bartram from Papua New Guinea (Bartram, 1959) and the new record of *U. phyllantha* from Macquarie Island (Seppelt, 1978). Recently, several species in this region are either treated as synonyms, including *Ulota dixonii* (= *U. viridis*, Fife, 2017; Ramsay, 2006), *U. fulva* (= *U. crispa*, Wang and Jia, 2012b), *U. lutea* (= *U. crispa*, Wang and Jia, 2012b) and *U. novae-seelandiae* (= *U. viridis*, Fife, 2017), or excluded from the Australia flora, *i.e.*, *U. pygmaeothecia* (= *U. luteola* (Hook. f. & Wilson) Wijk & Margad., Wang and Jia, 2018a). In conclusion, there are 14 *Ulota* species in Oceania so far.

Almost all the known species of *Ulota* in Oceania come from Australia, New Zealand, and Papua New Guinea. The surveys of other small islands seem to be very limited or even empty, such as Fiji, Vanuatu, and Solomon islands. Although three subantarctic islands (Auckland, Campbell, and Macquarie Islands) near New Zealand have been investigated (Vitt, 1979, 1974; Sainsbury and Allison, 1962), *Ulota* species has only been found in Macquarie Islands (Seppelt, 1978).

Europe:

The study of *Ulota* from Europe has the longest history; all species in this area were first described in the 19th century. The first reported species is *Orthotrichum crispum* (≡ *Ulota crispa*) (Hedwig, 1801), which is earlier than the establishment of the genus *Ulota* (Mohr, 1806). Later, Wahlenberg (1812) described a new species from Lapland (in North Europe), *Orthotrichum curvifolium* Wahlenb. (≡ *Ulota curvifolia* (Wahlenb.) Lilj). Meanwhile, *Orthotrichum ludwigii* (Brid.) Brid. (= *Ulota coarctata* (P. Beauv.) Hammar) was published by Bridel (1812). Soon, Smith (1813) and Bridel (1819) respectively added two new species from England and Denmark, namely *Orthotrichum hutchinsiae* Sm. (≡ *Ulota hutchinsiae* (Sm.) Hammar) and *U. phyllantha*. Subsequently, Hooker and Greville (1824) found *Orthotrichum drummondii* Hook. & Grev. (≡ *Ulota drummondii*) in Scotland. *Ulota bruchii* Hornsch. ex Brid. and *U. crispula* were reported respectively by Hornschuch and Bruch in 1827. Although its taxonomic status has changed many times in history (Caparrós *et al.*, 2016; Garilleti *et al.*, 2000; Smith and Proctor, 1993; Rosman-Hartog and Touw, 1987; Smith and Hill, 1975), they are still recognized in Europe recently (Caparrós *et al.*, 2016). More than 30 years later, *Ulota calvescens* from Ireland and *U. rehmannii* from Poland were published (Juratzka, 1864; Carrington, 1862). Soon after Schimper (1876) described another new species, *Ulota intermedia*. Similarly, this species has been in the status of variety or subspecies for a long time due to its obscure discrimination with *U. crispa* (Héribaud, 1899; Kindberg, 1897, 1883; Piré and Cardot, 1885), but has been restored recently (Caparrós *et al.*, 2016). In summary, there are 11 species of *Ulota* in Europe now.

The study of European *Ulota* is still uneven among different regions, although it started earlier than other continents. Countries in West and North Europe have generally been well investigated (Blockeel, 2017; Blockeel and Turner, 2013; Siebel and During, 2006; Smith, 2004, 1978; Augier, 1966; Nyholm, 1998, 1960; Delogne, 1884), while those in eastern Europe (except Latvia: Āboliņa, 1968; Russia: Fedosov and Ignatova, 2018), central and southern Europe (except Iberian Peninsula: Lara *et al.*, 2014; Albertos *et al.*, 2000) often have only some checklists (Austria: Köckinger *et al.*, 2012; Belarus: Rykovsky and Maslovsky, 2004; Bulgaria: Natcheva and Ganeva, 2005; Corsica: Sotiaux *et al.*, 2007; Croatia: Sabovljević, 2006; Greece: Preston, 1984; Italy: Privitera *et al.*, 2010; Aleffi *et al.*, 2008; Mediterranean: Ros *et al.*, 2013; Poland: Plášek *et al.*, 2016; Slovenia: Martincic, 2003).

Africa and surrounding islands:

Africa is the second-largest continent in the world after Asia; its surrounding islands mainly contain Madagascar, Réunion, and Madeira Islands. The first *Ulota* species in Africa is *U. fulva* described by Bridel (1826) from Réunion. Later, Hornschuch (1841) found another new species from South Africa, *i.e. Ulota ecklonii* (Hornsch.) A. Jaeger. Mitten (1870) added a new record of *Ulota calvescens* from Madeira. In 1955, Potier de la Varde described a new species again from Tanzania, namely *Ulota tanganyikae* P. de la Varde. However, *Ulota fulva* was recently reduced to *U. crispa* (Wang and Jia, 2012b), and *U. tanganyikae* was transferred into the genus *Orthotrichum* (Wang and Jia, 2014). Therefore, there are only three species of *Ulota* in Africa up to now.

The study of African *Ulota* is relatively weak. Although the preliminary investigation has basically covered the whole continent (Hedderson *et al.*, 2014; Ros *et al.*, 2013; Marline *et al.*, 2012; Dirkse and Losada-Lima, 2011; Wilbraham, 2008; Draper *et al.*, 2008, 2005; O'Shea, 2008, 2006, 1999, 1997; Germishuizen and Meyer, 2003; Wigginton, 2002; Bytebier and Chuah–Petiot, 2002; El-Saadawi *et al.*, 1999; Pócs and Lye, 1999; Ros *et al.*, 1999; Wigginton *et al.*, 1999; Magill and van Rooy, 1998; Dirkse *et al.*, 1993; van Rooy and Wyk, 1992; Ochi, 1973, 1972), only a few contain *Ulota* taxa. Moreover, most published works are only checklists and lack taxonomic study, which may be a reason why the number of *Ulota* species is very few in Africa. It will probably increase as the African *Ulota* becomes better known.

North America:

North America is the third largest continent, including Canada, the U.S.A., Mexico, and all Caribbean and Central American countries. The first species of

Ulota from this area were *Orthotrichum coarctatum* P. Beauv. (≡ *Ulota coarctata* (P. Beauv.) Hammar) and *O. americanum* P. Beauv. (= *U. hutchinsiae*), described by Palisot de Beauvois in 1805. Then, Mitten (1864a) reported two new species, *i.e.*, *Ulota barclayi* Mitt. and *U. americana* Mitt. (= *U. curvifolia*) and a new record, *i.e.*, *U. phyllantha*. Subsequently, another four new species were added respectively, including *Orthotrichum connectens* Kindb. (= *U. crispa*) (Kindberg, 1890), *U. megalospora* (Venturi, 1890), *U. obtusiuscula* Müll. Hal. & Kindb. (Müller and Kindberg, 1892) and *U. funstonii* Grout (= *U. drummondii*) (Grout, 1935). Two Japanese species were reported to disjunctively distribute in North America (Worley and Iwatsuki, 1970), *i.e.*, *Ulota japonica* and *U. reptans*, but later excluded by Vitt (2014, 2003). The only taxon known from Central America, *Ulota rhytiore* (B.H. Allen) F. Lara *et al.*, was first described as *Orthotrichum rhytiore* B.H. Allen (Allen, 2002) and transferred to *Ulota* by Albertos *et al.*, (2008). Finally, there are 11 species of *Ulota* in North America.

The *Ulota* species in North America are well studied. There are several versions of flora (Vitt, 2014; Crum and Anderson, 1981; Grout, 1946, 1935), but also outstanding monographs and revisions (Vitt, 1970). However, almost all of them are from the U.S.A., Canada, and northern Mexico; investigation in Central America and southern Mexico is relatively insufficient.

South America:

South America is the fourth largest continent, divided into 12 independent countries. It was once a disaster area for *Ulota* taxonomy because as many as 45 species were described or recorded in this area, including 29 published in the 19th century and 14 later. Most of them were lack of study for a long time and even was not mentioned after their original publications. The first species of *Ulota* reported from South America was *Orthotrichum magellanicum* Mont. (≡ *U. magellanica* (Mont.) A. Jaeger) by Montagne (1843). Soon after, he (1845) described another species, *Orthotrichum germanum* Mont. (≡ *Ulota germana* (Mont.) Mitt.) from Chile, while Müller (1845) almost simultaneously reported a new taxon, *Zygodon ventricosus* Müll. Hal. (≡ *U. ventricosa* (Müll. Hal.) Malta). Later, *Orthotrichum luteolum* Hook. f. & Wilson (≡ *Ulota luteola* (Hook. f. & Wilson) Wijk & Margad.), was published by Hooker and Wilson (1847) from Chile. Mitten is the author who published the most new species in this area, including eight in an article of 1859 alone and three in another work of 1869, which also added a new record of *Ulota phyllantha*. Most of these names were reduced in the later revisions. In addition to *Ulota ventricosa* (1845), Müller also published seven new species from South America successively (1862, 1885, 1897), but he apparently hesitated to decide whether they belong to *Ulota* or *Orthotrichum*, because the name of these two genera is shown at the same time. Although he contributed the second most new species of *Ulota* in this region, later studies suggested that most of these species did not belong to *Ulota*. Besides Mitten and Müller, other authors have also reported sporadically some species of *Ulota* in this area, including Hooker (1867), Ångström (1872), Jaeger (1874), Bescherelle (1885), Dusén (1903), and Cardot (1905). They together added nine species, most new to science but none confirmed by later studies. The first comprehensive revision of *Ulota* in South America was done by Malta (1927), and it was the only revision for quite a long time. He accepted 17 names, including six new to science. In the 21st century, the publication of new species is not so random, but Garilleti *et al.*, (2020, 2015, 2012) still found four new species through recent fieldwork, namely *Ulota billbuckii* Garilleti, Mazimpaka & F. Lara, *U. maltiana* Garilleti & F. Lara, *U. larrainii* Garilleti, Mazimpaka & F. Lara and *U. streptodon* Garilleti, Mazimpaka & F. Lara. Recently, we (2016) revised the genus *Ulota* in this region in detail. After reducing eight names and adding a new record, 14 species were ultimately recognized by us. As stated above, the classification of *Ulota* in South America has been significantly improved, and a total of 16 species are distributed in this area.

Islands far from continents

Ulota species are also recorded in a few islands far from continents, containing Azores, Hawaii, and Kerguelen. Firstly, Müller (1883) described *Orthotrichum phyllanthoides* Müll. Hal. (≡ *Ulota phyllanthoides* (Müll. Hal.) Kindb.), based on the specimen from the Kerguelen Islands in the southern Indian Ocean. Then, *Ulota calvescens* was reported from Azores islands in the Macaronesia region of the North Atlantic Ocean archipelago (Allorge and Persson, 1938). Until 1971, *Ulota cervina* Hoe & H.A. Crum from Hawaii islands in the North Pacific Ocean was described (Hoe and Crum, 1971), which was recently reduced as a synonym of *U. crispa* by us (Wang and Jia, 2012b). Therefore, there are three *Ulota* species scattered on isolated islands in three oceans.

Chapter 3

Material and Methods

This study is specimen-based, and wherever possible, type specimens have been examined. At present, nearly 300 type specimens and more than 4200 non-type specimens have been studied. These specimens are mainly obtained from 41 herbaria around the world, including AKPM, AM, B, BBSUK, BISH, BM, BP, C, CANM, CHR, DUKE, E, FH, FI, H, HBG, HIRO, HO, HYO, IBK, IFP, JE, KUN, KYO, L, M, MICH, MO, NICH, NSW, NY, OSA, PC, PE, PRE, RB, S, TNS, UBC, UC, and WELT. The type specimens are referred to more than 100 names. A few types have not been available yet, because either they are not located, or they are too old to be borrowed. The non-type specimens, except for some (ca. 560) unidentified due to the barely legible handwriting, are from six continents, including more than 1500 specimens from Europe, nearly 1000 from North America, ca. 630 specimens from Asia, ca. 230 specimens from Oceania, ca. 210 specimens from South America and less than 20 specimens from Africa and its surrounding islands. Besides that, these non-type specimens were collected from 43 countries in total, and the top ten are the following: Finland, the U.S.A., China, Canada, the U.K., Chile, Sweden, Japan, Australia, and Norway.

All specimens were observed under a light microscope, and all type specimens and some non-type specimens in good condition were photographed. All the diagnostic characters used here are distinguishable by the naked eye or light microscope.

The scanning electron microscope (SEM) was carried out when the materials were sufficient. Fifty types and 13 non-type specimens were selected for the study of ornamentation on the surfaces of peristome and spores, sometimes papillose on leaf cells. Most of them are new to science generated by us. The dry materials were soaked in water for a while and then stuck on aluminum stubs with double sided tape. When the materials were dry, they were coated with gold and then visualized under a Hitachi S-4800 scanning microscope at an accelerating voltage of 10 kV and a working distance of 25–29 mm.

Some quantitative characters were measured in this study. The measurement data of most species come from at least three populations, even more than ten populations for three species, *i.e. Ulota crispa*, *U. fuegiana* Mitt. and *U. megalospora*. For leaf length, mostly 30–100 samples were selected, the least is *Ulota rhytiore*, only five ones. For the length of the perichaetial leaf, more than ten samples were measured in

DOI: 10.1051/978-2-7598-2911-8.c003
© Science Press, EDP Sciences, 2023

half of the species; the most is *Ulota perichaetialis*, up to 50 ones. For the size of leaf cells, 60–200 samples were measured in most species; the least is *Ulota macrodontia* Dixon & Malta, with only 30 ones. For seta length, more than ten samples were included in half species, and only one sample was chosen in three species, *i.e. Ulota eurystoma*, *U. pycnophylla* Dusén ex Malta and *U. rhytiore*. For capsule length, 1/3 species measured in more than ten samples, 1/3 species measured in 5–9 ones, and the remaining 1/3 species measured in less than five ones. For spore diameter, 50–200 samples were measured for most species, 30–50 ones for a few species, less than 20 ones in *Ulota streptodon* and *U. rubella* and no spore in *U. eurystoma*.

In this work, type information is given for all species, but not all type material has been examined. Examination of type material is indicated by the citation of an herbarium acronym (see Index Herbariorum) and an exclamation mark at the end of the type information. To facilitate use, the species are arranged alphabetically within each section. Species descriptions are detailed and comprehensive. For each species, important previously published illustrations are given. Short, concise habitats are recorded based on our field experience or specimens unless otherwise noted. The world distribution range of each species is determined by the examined specimens. Almost all species for which no type specimen has been examined are placed in a "Doubtful taxa" section.

Chapter 4

Taxonomy

4.1 Morphology

Plants — The plant color is greatly diverse in *Ulota*, and the basal part in a plant is often deeper than the upper part (figure 1). For example, the upper part often varies from light yellow, yellowish green, golden yellow to dark-yellow, while the lower part is from brown, dark brown to black. The epiphytic populations in *Ulota* vary in color, but the saxicolous ones are often consistently brown to black (figure 1m,n). Most species in *Ulota* are 1–3 cm in height. The smallest species are often around 0.5 cm, such as *U. barclayi*, *U. japonica*, *U. macrocalycina*, *U. megalospora*, and *U. pycnophylla*, while the largest species can reach 9 cm, which is *U. splendida* from Papua New Guinea. The stems in *Ulota* species are often branched, without a central strand (figure 2). They are sometimes erect or ascending, sometimes the main stem is creeping, and the branches are erect. The creeping stems for identification of some species have been sometimes suggested (Ramsay, 2006), and we found that this character is more common than expected in the genus, except for the previously known species (*Ulota macrocalycina*, *U. magellanica* and *U. viridis*), also including *U. drummondii*, *U. luteola*, *U. pusilla*, *U. rehmannii*, and *U. reptans.*

Leaves — The leaves in most *Ulota* species are flexuose or crisped to various degrees when dry, a few are erect to flexuose, such as *U. coarctata*, *U. curvifolia*, *U. drummondii*, *U. magellanica*, and *U. membranata*, and a few are erect and appressed, including *U. hutchinsiae* and *U. macrocalycina* (figure 1). The leaf states in moist change little among different species, from wide-spreading to patent. The leaves are generally lanceolate, with more or less widened bases (figure 3). The leaf bases are often round, and a few are ovate, such as *Ulota macrocalycina*, *U. splendida*, and *U. streptodon.* The leaf apexes are mostly acuminate to long acuminate, with few acute, including *Ulota barclayi* and *U. macrocalycina*, and few sinuose or tortuose, such as *U. splendida* and *U. streptodon.* The leaf margins are entire and plane, sometimes partially recurved. All species have single strong costa, reaching the apex or disappearing just below the apex. The leaf size in *Ulota* varies greatly. Most of them are 1–3 mm in length, with the largest ones up to 5 mm from *Ulota rhytiore* and the smallest ones less than 1 mm, such as *U. gigantospora*,

DOI: 10.1051/978-2-7598-2911-8.c004
© Science Press, EDP Sciences, 2023

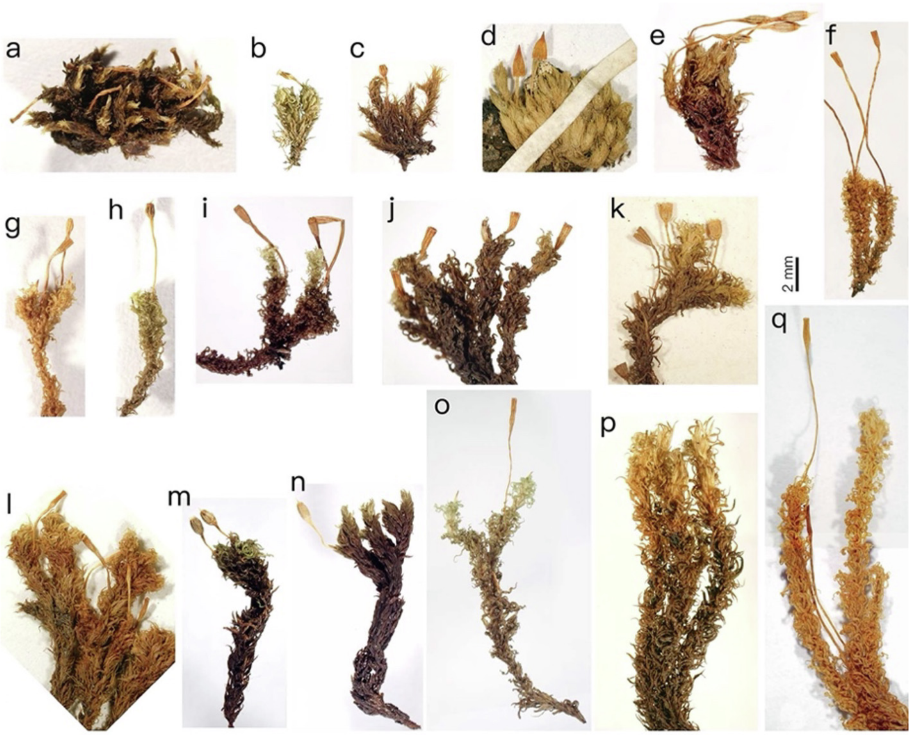


FIG. 1 – Plant diversity in *Ulota* species. a. *U. barclayi*. b. *U. japonica*. c. *U. yakushimensis*. d. *U. macrocalycina*. e. *U. drummondii*. f. *U. angusti-limbata*. g. *U. yunnanensis*. h. *U. gigantospora*. i. *U. crispula*. j. *U. perbreviseta*. k. *U. robusta*. l. *U. fuegiana*. m. *U. curvifolia*. n. *U. hutchinsiae*. o. *U. panchengiana*. p. *U. perichaetialis*. q. *U. splendida*. (all successively from: *W. B. Schofield 86158* [non-type] in DUKE, holotype in FH, holotype in FH, isotype in BM, *M. Higuchi 1192* [non-type] in PE, holotype in FH, holotype in E, holotype in E, *Y. Jia 09720* [non-type] in PE, *R. Toyama 3186* [non-type] in KYO, isotype in FI, isotype in E, *Afonina s.n.* [non-type] in PE, *D. H. Vitt* [non-type] in PE, holotype in PE, lectotype in WELT, and isotype in MICH).

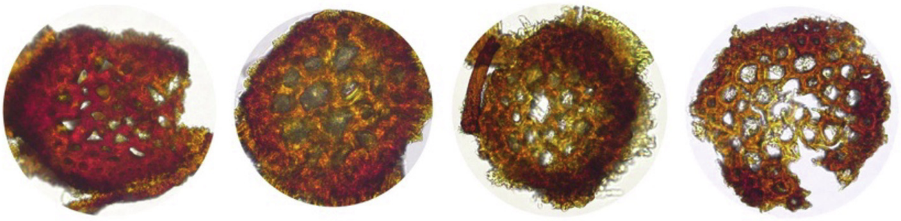


FIG. 2 – Stem cross-section of *Ulota*. Species from left to right are *U. crispa*, *U. curvifolia*, *U. gymnostoma*, and *U. panchengiana*. (all successively from: *Q.-H. Wang 2581*, *M. Sulayman 2287*, *T. Xu & C. Wang 20190423-1* and *Q.-H. Wang 2677*, all non-type in PE).

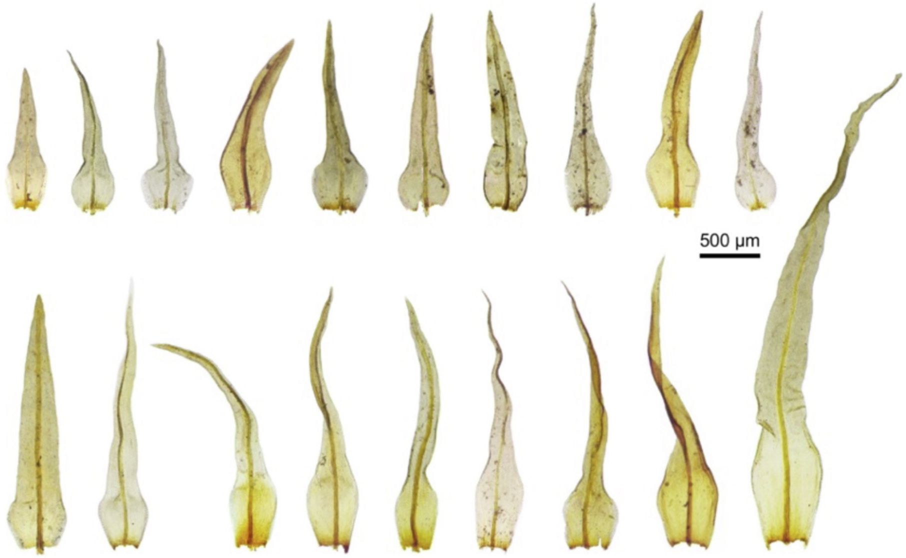


Fig. 3 – Leaf diversity in *Ulota* species. The top line from left to right are: *U. macrocalycina*, *U. megalospora*, *U. pusilla*, *U. hutchinsiae*, *U. yakushimensis*, *U. reptans*, *U. rehmannii*, *U. viridis*, *U. curvifolia*, *U. magellanica*; the bottom line from left to right are: *U. drummondii*, *U. coarctata*, *U. membranata*, *U. novo-guinensis*, *U. cochleata*, *U. streptodon*, *U. perichaetialis*, *U. rubella*, *U. splendida.* (all successively from isotype in BM, *W. B. Schofield & J. H. Lyford 72252* [non-type] in UBC, *T. Halle et C. Skottsberg* [non-type] in S, *R. R. Ireland 15528* [non-type] in UBC, *Z. Iwatsuki* [non-type] in S, isotype in E, *Q. Gao 7507* [non-type] in IFP, *G. O. K. Sainsbury* [non-type] in S, *M. Sulayman 98-K151* [non-type] in PE, lectotype in PC, lectotype in E, *M. Dickron* [non-type] in BM, *W. A. Weymouth 22* [non-type] in HO, holotype in FH, *L. Rodway 1524* [non-type] in HO, *A. Hollermager 1668* [non-type] in PC, lectotype in WELT, holotype in FH and holotype in FH).

U. megalospora, and *U. reptans* (figure 4). The perichaetial leaves are mostly 2–4 mm, usually hardly or slightly differentiated, only a few are significantly longer than vegetative leaves, such as *Ulota germana* and *U. perichaetialis.*

Leaf cells — The upper and middle leaf cells in *Ulota* are uniformly rounded, hexagonal and oblong, with distinctly thickened walls. The only exception is *Ulota calvescens*, which often has 3–4 rows of elongated cells inside the margin, ascending above the base, usually up to the central part of the leaf. Most of the cells are covered with papillose, high or low, single or multiple, branched or unbranched (figure 5). There are only two species so far, usually with smooth laminal cells, namely the European *Ulota calvescens* and the Chinese *U. gymnostoma.* The basal leaf cells in *Ulota* are all smooth, but the marginal cells often markedly differentiate from the inner ones in shape, color, and wall thickness. The basal inner cells in most species are very long and narrow (rectangular, elongate-rectangular, or vermicular) with

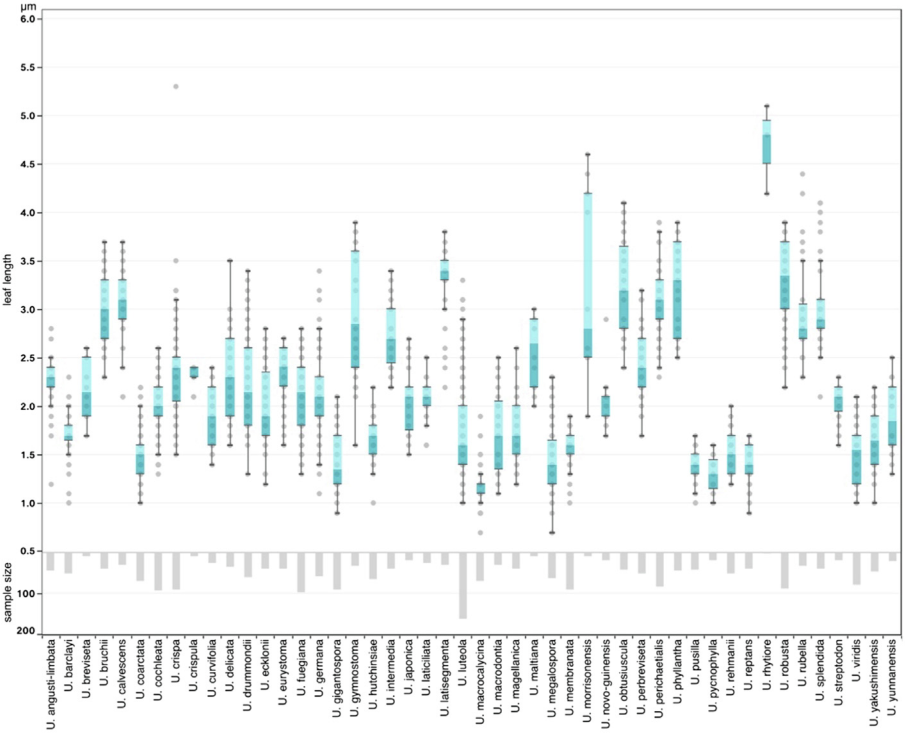


FIG. 4 – Leaf length in *Ulota* species. The gray bars represent sample size in each species.

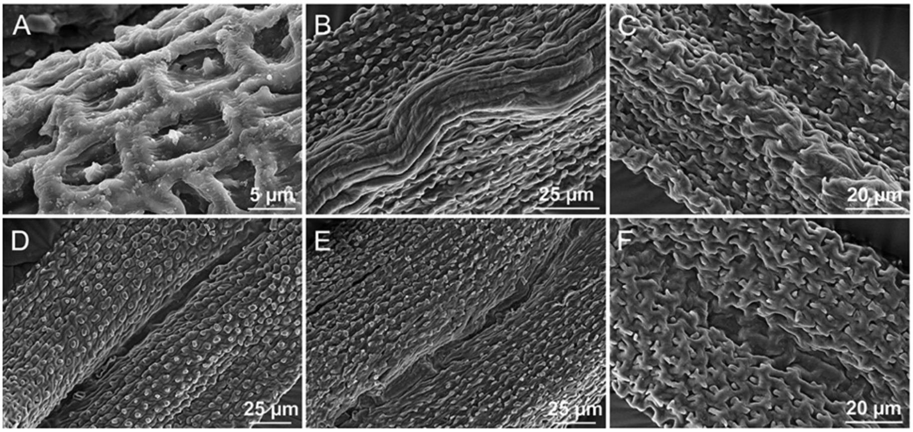


FIG. 5 – Papillose on middle and upper leaf cells in some *Ulota* species. A and D–F, The ventral surfaces; B–C, The dorsal surfaces. A, *U. eurystoma*; B, *U. obtusiuscula*; C, *U. maltiana*; D, *U. viridis*; E, *U. obtusiuscula*; F, *U. maltiana*. (all from: A, isotype in KYO; B and E, isotype in MO; C and F, *P. Dusén 434* [non-type] in H; D, isotype in H).

strongly thickened walls, while in a few species, the cells are relatively shorter (rectangular or elongate-rectangular) with slightly thickened walls, such as *Ulota barclayi* and *U. japonica* (figures 6d,e and 7). The basal leaf cells from the middle to margins usually become shorter, the walls become thinner, and the color becomes lighter; even the most marginal rows of cells are often hyaline. These hyaline cells are usually thickened only in transversal walls; some of them are slightly, equally thickened in both longitudinal and transversal walls, and even a few are thin-walled (figure 6). The last case mostly occurs in South American species, such as *Ulota macrocalycina*, *U. pusilla* and *U. pycnophylla* (figure 6f,g). In most *Ulota* species, there are more than four rows of hyaline cells at basal leaf margins, forming distinctly hyaline bands. But there are some species with only 1–3 rows, such as *Ulota angusti-limbata*, *U. luteola*, *U. magellanica*, and *U. megalospora*, even in a few species the hyaline cells are absent, such as *U. hutchinsiae* and *U. phyllantha* (figure 6).

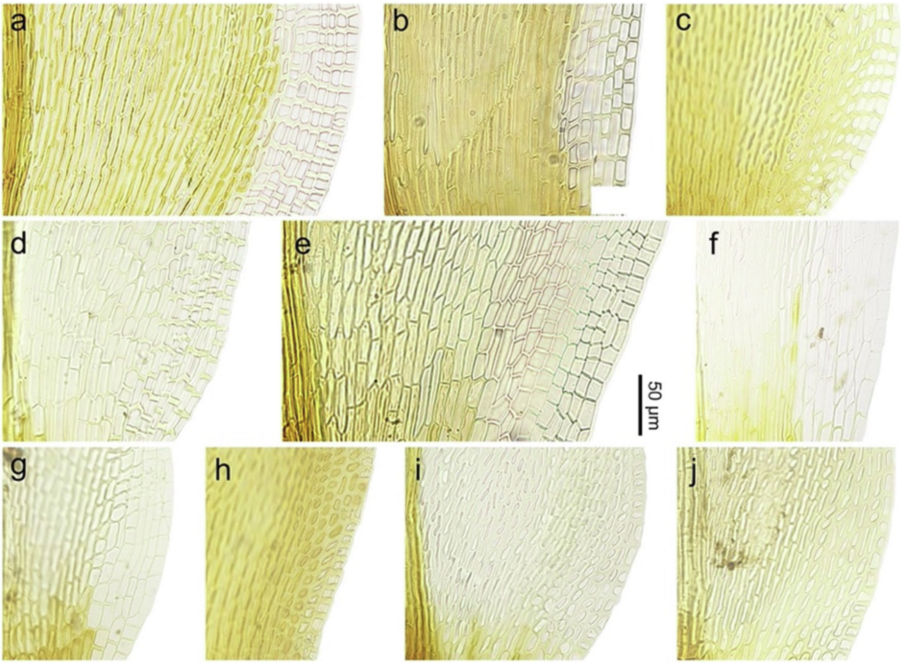


Fig. 6 – Basal leaf cells in some *Ulota* species. a. *U. maltiana.* b. *U. crispula.* c. *U. viridis.* d. *U. japonica.* e. *U. barclayi.* f. *U. macrocalycina.* g. *U. pusilla.* h. *U. hutchinsiae.* i. *U. megalospora.* j. *U. magellanica.* (all successively from *P. Dusén 434* [non-type] in S, lectotype in B, *G. O. K. Sainsbury* [non-type] in S, holotype in FH, isotype in FH, isotype in BM, *T. Halle et C. Skottsberg* [non-type] in S, *R. R. Ireland 15528* [non-type] in UBC, *W. B. Schofield & J. H. Lyford 72252* [non-type] in UBC and *R. R. Ireland & G. Bellolio 36077* [non-type] in MO).

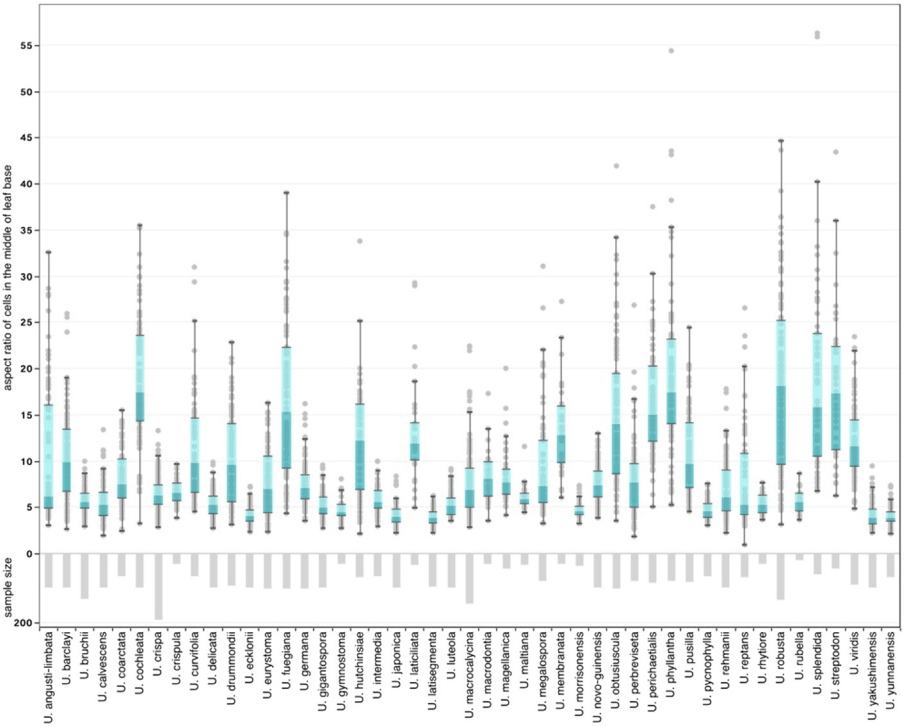


FIG. 7 – The ratio of longitudinal length to transverse length of basal inner leaf cells in *Ulota* species. The gray bars represent sample size for each species.

Gemmae — There is only one species in *Ulota* so far producing gemmae frequently, *i.e. U. phyllantha*, and it's the main way to reproduce for this species. No gemmae have been seen in other species during this study, but their sporophytes are common. In *Ulota phyllantha*, the gemmae are usually clustered at the tip of the leaves near the top of branches. The gemmae are cylindrical or clubbed, orange or red, mostly composed of 4–10 uniserial cells, unbranched (figure 8).

Capsules — All capsules in *Ulota* are located at the end of branches, and most are obviously higher than the perichaetial leaves, whereas in a few species (*U. barclayi*, *U. gymnostoma*, *U. perbreviseta*, and *U. rhytiore*) the capsules are always or sometimes emergent and in *U. perichaetialis* its capsules are even immersed (figures 9 and 10).

The capsule shape in *Ulota* generally refers to the dry condition when the spores have been released, because this is the most common state we saw. If the shape is conspicuously different between dry and wet, it will be described separately in this work. Considering this, the capsules in most *Ulota* species are short-cylindrical, cylindrical, or long-cylindrical, while the ones in a few species are fusiform (*U. gymnostoma and U. rhytiore*), obovoid (*U. eurystoma* and *U. membranata*), pyriform (*U. coarctata*) and subglobose (*U. yakushimensis*) (figures 10 and 11).

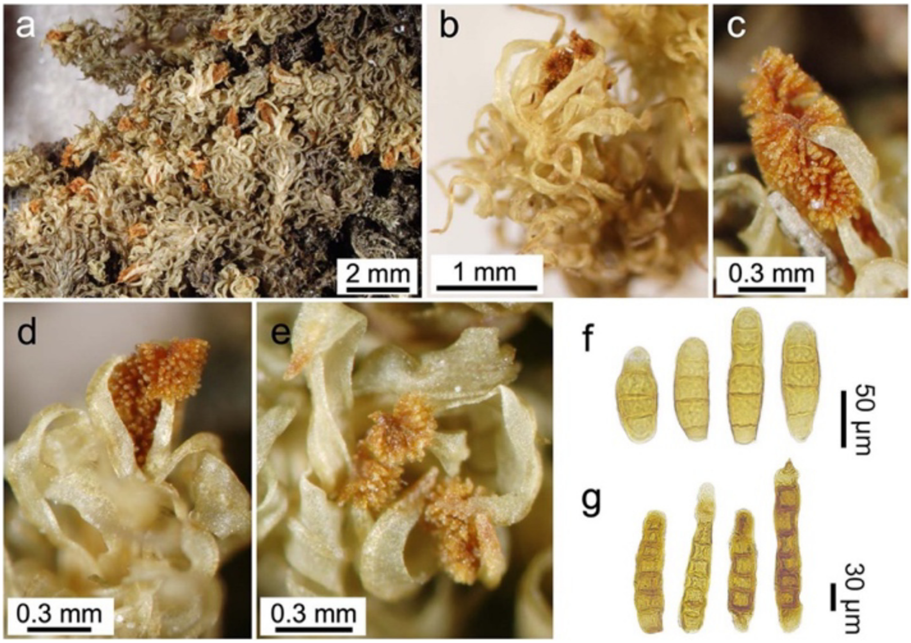


FIG. 8 – Gemmae in *Ulota phyllantha.* (a and c–f from *s.coll.* [non-type] in HBG, b from *W. B. Schofield 100736* [non-type] in DUKE, and g from *Roivainen s.n.* [non-type] in MICH).

The capsules generally consist of two parts, an urn and a neck, although there often lack a clear delimitation between them. The neck length is often described as the capsules in dry, and not distinct in most *Ulota* species, gradually or abruptly narrowed to the seta. Only a few species have a markedly long neck, including *Ulota bruchii*, *U. drummondii*, *U. megalospora*, and *U. obtusiuscula*. The neck length sometimes varies greatly in dry and wet, empty and full, as well as different ages. It usually seems longer in empty, dry, or older ages. Therefore, these factors sometimes cause confusion in the identification of some species, such as *Ulota bruchii* and *U. crispa*. We, therefore, should be very cautious about using it as a classification criterion.

The capsules in all *Ulota* species can more or less constrict when they are dry and empty, and thus form eight longitudinal ridges or furrows of different lengths. In most species, their capsules constrict moderately to strongly when dry, while in some species, they only constrict slightly, such as *Ulota obtusiuscula*, *U. perbreviseta*, *U. pusilla*, *U. reptans*, and *U. robusta*, and in a few species, such as *U. cochleata* and *U. eurystoma*, their capsules (almost) do not constrict when dry and their eight longitudinal ridges are obscure even if they are present. Most capsules in *Ulota* constrict evenly, and thus the longitudinal ridges are (almost) as long as the whole urn or at least half urn. However, there are a few species in which the capsule contractions near the mouth are obviously stronger than that at the lower part, including *Ulota delicata*, *U. drummondii*, *U. panchengiana*, and *U. streptodon*, or even only constrict near the mouth and smooth in the lower part, such as *U. coarctata*, *U. gymnostoma*, and *U. rhytiore* (figure 10).

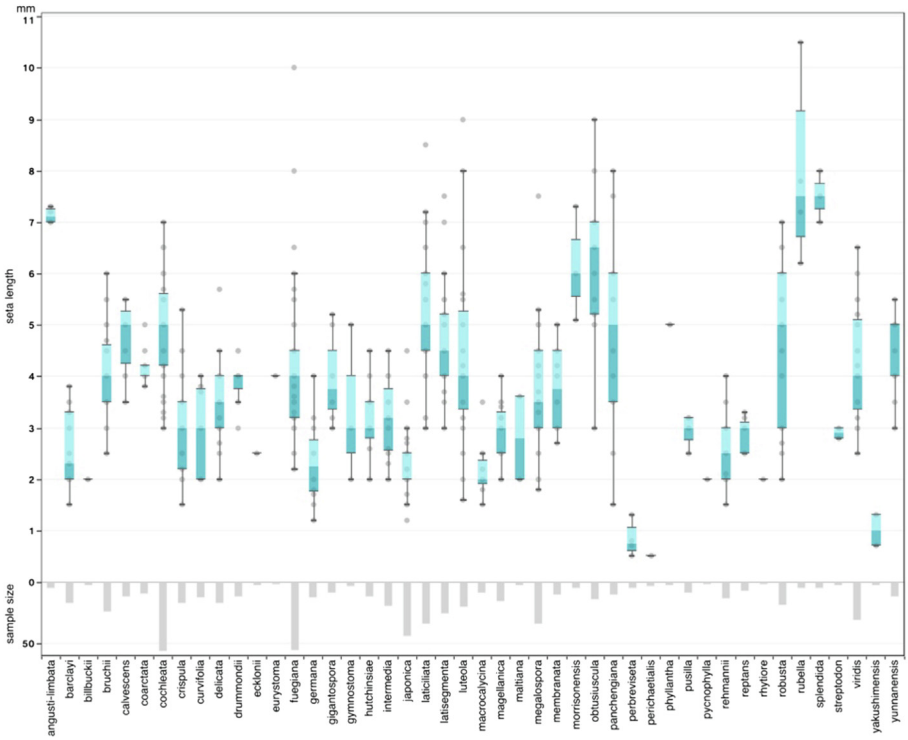


Fig. 9 – Seta length in *Ulota* species. The gray bars represent sample size for each species.

The capsules in *Ulota* often alternatively appear as furrows and ridges when dry, and the longitudinal walls of exothecial cells are thin and thickened accordingly. The ridges are eight per capsule, composed of four rows, occasionally 2–3 or 5–6 rows of cells with thickened longitudinal walls to some extent. Their color is often darker than the ones in furrows and thus forming eight longitudinal bands. When the capsule is dry, the stronger it constricts, the more prominent the ridges are and the clearer the bands are, such as *Ulota delicata* and *U. japonica*; and vice versa, such as *U. eurystoma*.

Stomata — Only superficial stomata (*vs.* immersed ones in *Orthotrichum*) have been found in the genus *Ulota* so far (figure 12). Most of them are composed of two kidney-shaped guard cells around a pore (figures 12a,b and 13). In a few cases, there will be abnormally four guard cells (figure 12d), and even a round cake-shaped cell with no pore in the middle (figure 12e,h). There are also some variations in the size (figure 12f) and color (figure 12e,g,h) of stomata, but no regular pattern has been found during this study.

There are generally two kinds of stomata position; one is on the urn, and the other is at the base of the urn or on the junction between the urn and neck. This is an important diagnostic character for some species, such as *Ulota panchengiana*.

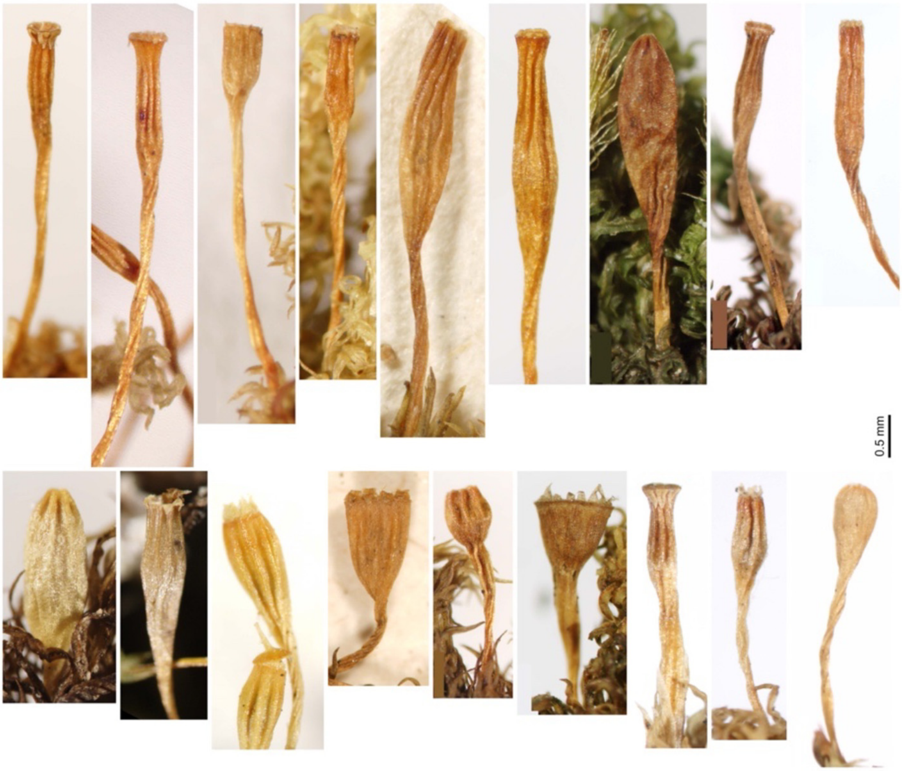


Fig. 10 – Capsule diversity in *Ulota* species. The top line from left to right are: *U. novo-guinensis*, *U. laticiliata*, *U. yunnanensis*, *U. phyllantha*, *U. drummondii*, *U. splendida*, *U. gymnostoma*, *U. crispa*, *U. panchengiana*; the bottom line from left to right are: *U. rhytiore*, *U. megalospora*, *U. membranata*, *U. robusta*, *U. yakushimensis*, *U. eurystoma*, *U. barclayi*, *U. delicata*, *U. coarctata*. (all successively from holotype in FH, *J. K. Bartlett* [non-type] in AM, holotype in E, *W. B. Schofield 100736* [non-type] in DUKE, lectotype in E, holotype in FH, holotype in H, *S.-J. Li 116* [non-type] in PE, holotype in PE, holotype in NY, *W. B. Schofield 72346* [non-type] in UBC, *W. A. Weymouth 22* [non-type] in HO, isotype of *U. bellissima* in FI, holotype in NICH, isotype in KYO, isotype in FH, *P.-C. Chen et al. 7047b* [non-type] in PE, *H. Crum 9873* [non-type] in PE).

The number of stomata per capsule in *Ulota* has remained poorly known. Erzberger (2003) once studied the stoma number of four *Ulota* species based on more than 600 capsules. He stated that this character has no taxonomic value due to its great variability to environments. More than 200 capsules from 39 species were investigated in this study (figure 14). The number of stomata per capsule is mostly 10–50; a few are less than ten, such as *Ulota macrocalycina* and *U. megalospora*, or more than 60, including *U. latisegmenta*, *U. obtusiuscula* and *U. splendida*. The maximum number of stomata in a single capsule is 146 in *Ulota cf. robusta* (*C.-Y. Yang 120-b*, PE). The stoma number often varies in a species, and no regular pattern has been observed.

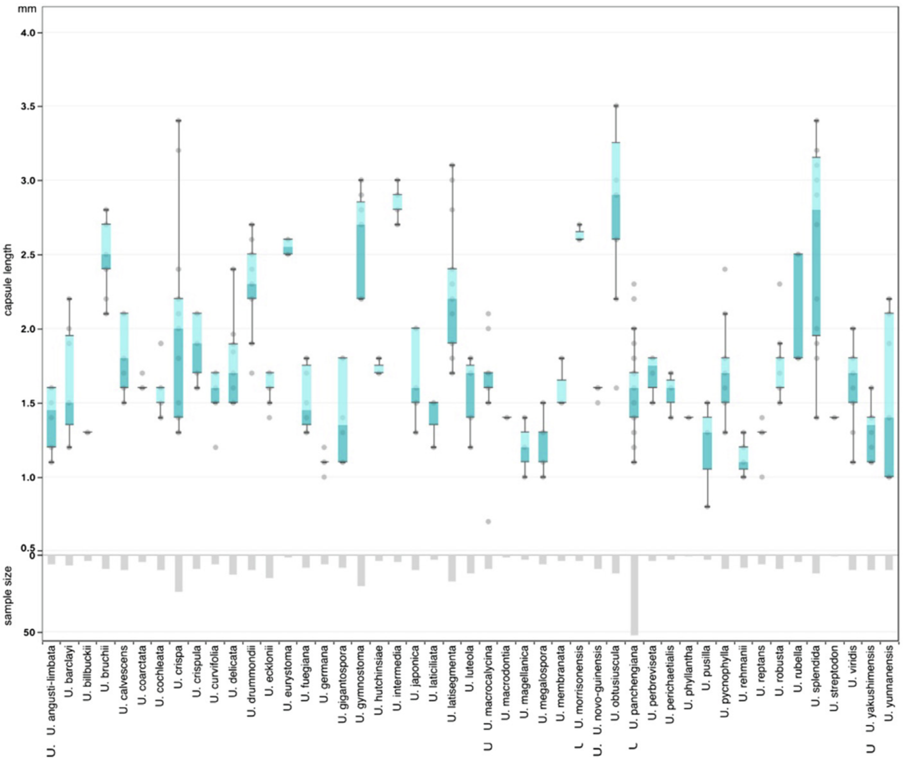


FIG. 11 – Capsule length in *Ulota* species. The gray bars represent sample size for each species.

Peristome — All species in *Ulota* have well-developed peristome, except *U. gymnostoma* and *U. rhytiore* whose peristome are lacking or rudimentary. Most peristome in *Ulota* are double-layer, containing exostome teeth and endostome segments; only a few are single-layer, *i.e.* endostome segments are absent or rudimentary, including *U. coarctata*, *U. drummondii*, *U. perichaetialis*, *U. streptodon*, and *U. yakushimensis*. The peristome in *Ulota* is indispensable for interspecific classification, especially the endostome segments.

Exostome teeth

Most species in *Ulota* have 16 well-developed teeth and are often united into eight pairs. The colour of the teeth irregularly varies from light yellow to dark yellow (figure 15). The teeth are narrow-lanceolate or narrow-triangular (figure 15), sometimes cancellate on the upper part, often recurved and lying on the exothecium when dry, rarely erect or spreading when the opercula are opened before full maturity. But in *Ulota coarctata*, *U. delicata*, *U. eurystoma*, *U. streptodon*, and *U. yakushimensis*, the teeth are variably incurved, erect or spreading, or deflexed when dry and mature. It is noteworthy that the exostome teeth in *Ulota macrodontia* are described as always incurved, even after several hydrating and drying cycles (Garilleti *et al.*, 2021).

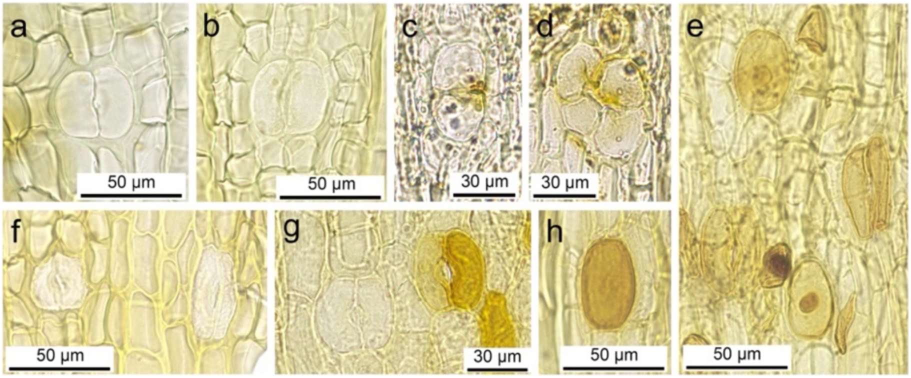


FIG. 12 – Micrographs of stomata in *Ulota* species. a. *U. megalospora*. b. *U. ecklonii*. c and d. *U. crispa* (Hawaii), e and h. *U. obtusiuscula*. f. *U. novo-guinensis*. g. *U. intermedia*. (all successively from *W. B. Schofield & J. H. Lyford 72252* [non-type] in UBC, isotype in S, holotype of *U. cervina* in MICH, isosyntype in FH, holotype in FH, *N. Bryhn s.n.* [non-type] in NSW and isosyntype in NY).

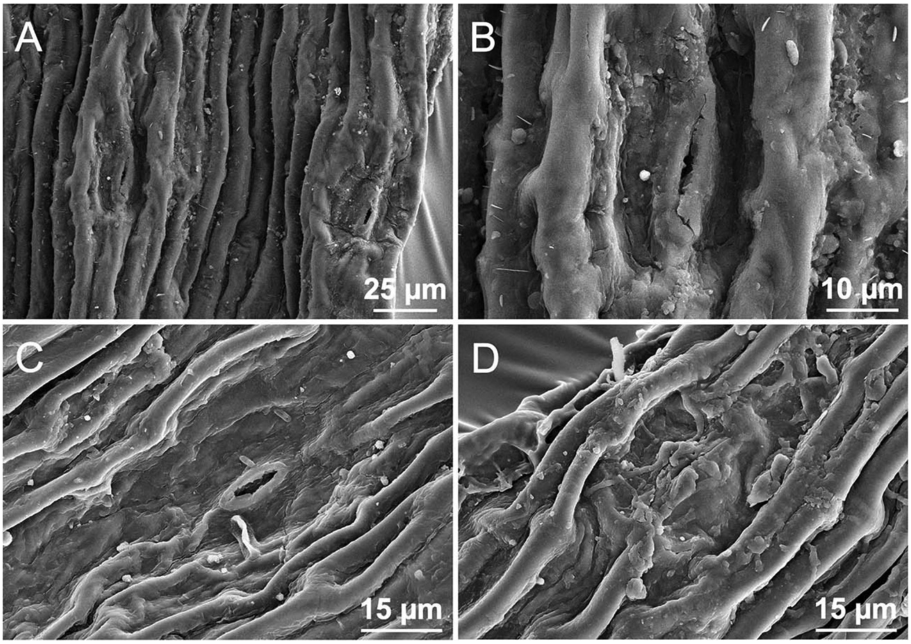


FIG. 13 – Stomata in some *Ulota* species. A–B, *U. laticiliata*; C, *U. maltiana*, D, *U. yakushimensis*. (A–B from lectotype in FH, C from *P. Dusén 434* [non-type] in H[4334009], D from holotype in NICH).

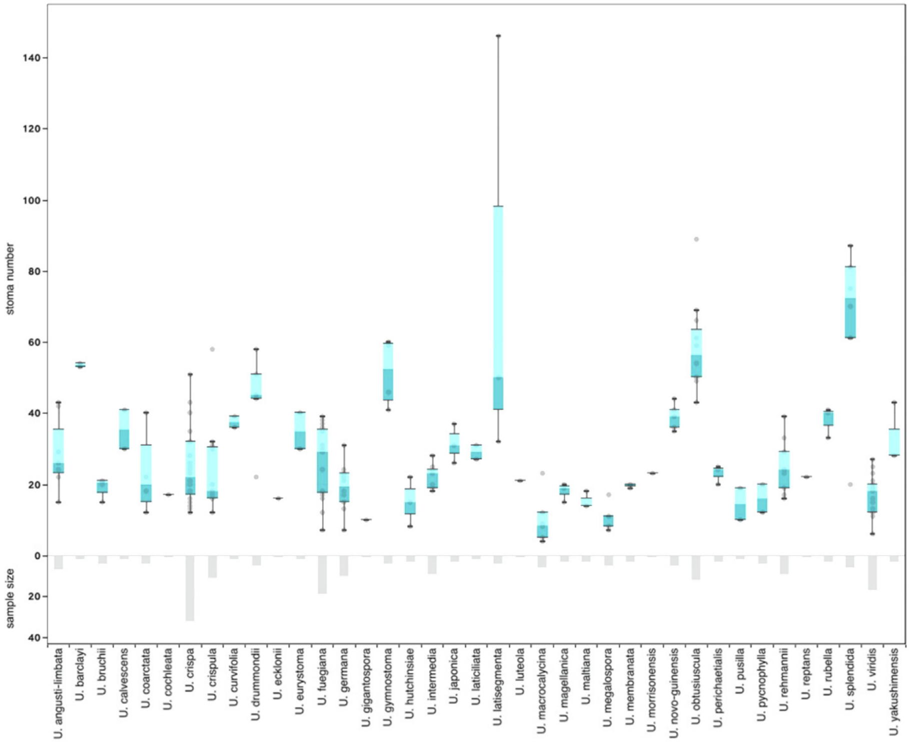


FIG. 14 – Stoma number per capsule in some *Ulota* species. The gray bars represent sample size for each species.

But we have never seen any species in *Ulota* whose exostome teeth are always, or at least mostly, incurved when dry and mature. This is quite uncommon in the whole genus. According to our observations, the exostome teeth sometimes tend to bend inward when the capsules are not completely mature, which seems to be the case in the pictures provided by Garilleti *et al.* (2021) where almost all the opercula are not completely detached. Although they listed more than 20 specimens, they did not emphasize whether they were all or mostly so. Little materials are available for us so far, and we think that this apparently unnatural case that was likely caused by immaturity needs more evidence.

Under the light microscope, the ornamentation on the outer surface of the teeth in *Ulota* varies little, mostly papillose thoroughly or papillose below and striate-papillose above. Only a few species have teeth with distinct striate, including *Ulota curvifolia*, *U. ecklonii*, *U. rehmannii*, and *U. yunnanensis*, or with wrinkles as in *U. eurystoma*. Similarly, the ornamentation on the inner surface of the teeth also varies indistinctly and is weaker than that on the outer surface (figure 15). In most cases, there is striate below and papillose above on the inner surface of the teeth. A few species have remarkable striate, such as *Ulota calvescens*, or strong papillose, such as *U. drummondii*.

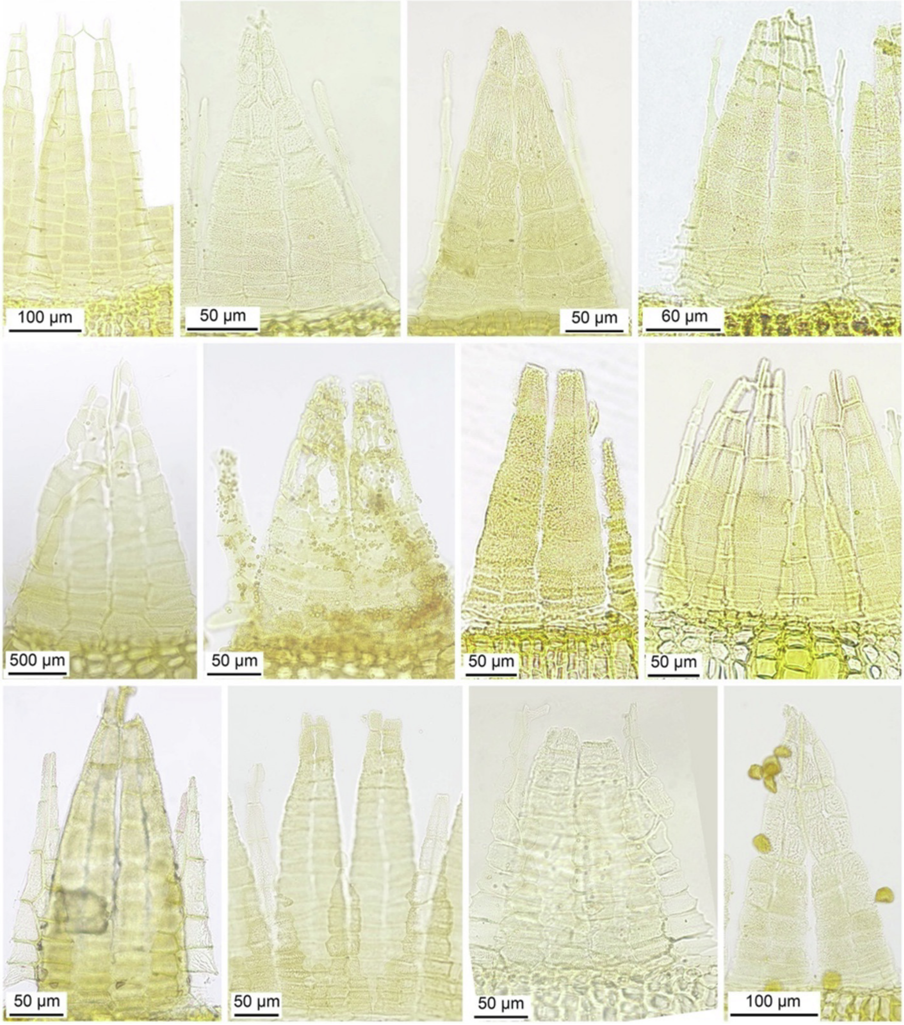


FIG. 15 – Peristome structure in some *Ulota* species under light microscope. The top line from left to right are: *U. calvescens*, *U. viridis*, *U. rehmannii*, *U. cochleata*; the middle line from left to right are: *U. curvifolia*, *U. gigantospora*, *U. macrodontia*, *U. maltiana*; the bottom line from left to right are: *U. laticiliata*, *U. latisegmenta*, *U. magellanica*, *U. drummondii*. (all successively from: *D. M.* [non-type] in H, *G. O. K. Sainsbury* [non-type] in S, *8hii* [non-type] in BP, isotype in HO, *M. Sulayman 98-K151* [non-type] in PE, *X.-J. Li 9075* [non-type] in KUN, *M. Gusinde s.n.* [non-type] in S, *P. Dusén 434* [non-type] in H, *A. J. Fife 11519* [non-type] in CHR, holotype in PE, *R. R. Ireland & G. Bellolio 36077* [non-type] in MO and lectotype in E).

Under the SEM, the ornamentation of the teeth certainly has greater variations (figures 16 and 17). Generally, there is papillose below and striate or striate-papillose above on the outer surface, but in *Ulota phyllantha* it is a remarkable striate below

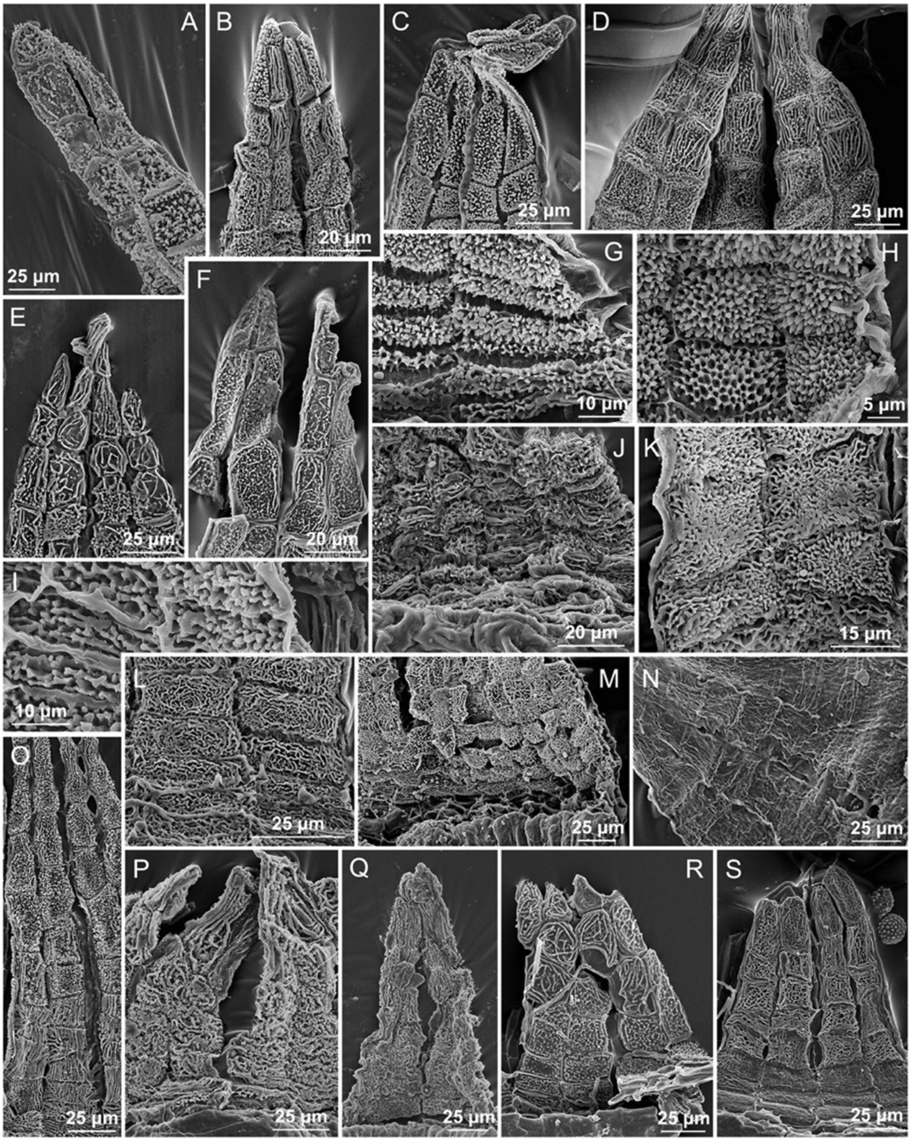


FIG. 16 – The outer surface of exostome teeth in some *Ulota* species. A–F, The upper part; G–N, The lower part; O–S, The whole part. A, *U. drummondii*; B, *U. magellanica*; C, *U. macrocalycina*; D, *U. calvescens*; E, *U. megalospora*; F, *U. rehmannii*; G, *U. barclayi*; H, *U. pusilla*; I, *U. gigantospora*; J, *U. magellanica*; K, *U. japonica*; L, *U. ecklonii*; M, *U. membranata*; N, *U. eurystoma*; O, *U. phyllantha*; P, *U. coarctata*; Q, *U. yakushimensis*; R, *U. yunnanensis*; S, *U. curvifolia*. (all successively from lectotype in E, *N. J. Andersson* [non-type] in S, isotype in BM, isotype in M, *W. B. Schofield & R. J. Belland no.84609* [non-type] in UBC, *J. Breiveer* [non-type] in HBG, *W. B. Schofield 86158* [non-type] in DUKE, holotype in H, holotype in E, *N. J. Andersson* [non-type] in S, holotype in FH, isotype in S, isotype in HO, isotype in KYO, *W. B. Schofield 100736* [non-type] in DUKE, *J. Shaw 15435-1* [non-type] in DUKE, isotype in NUM, *L.-S. Wang 83-1173a* [non-type] in PE and *M. Sulayman K151* [non-type] in PE).

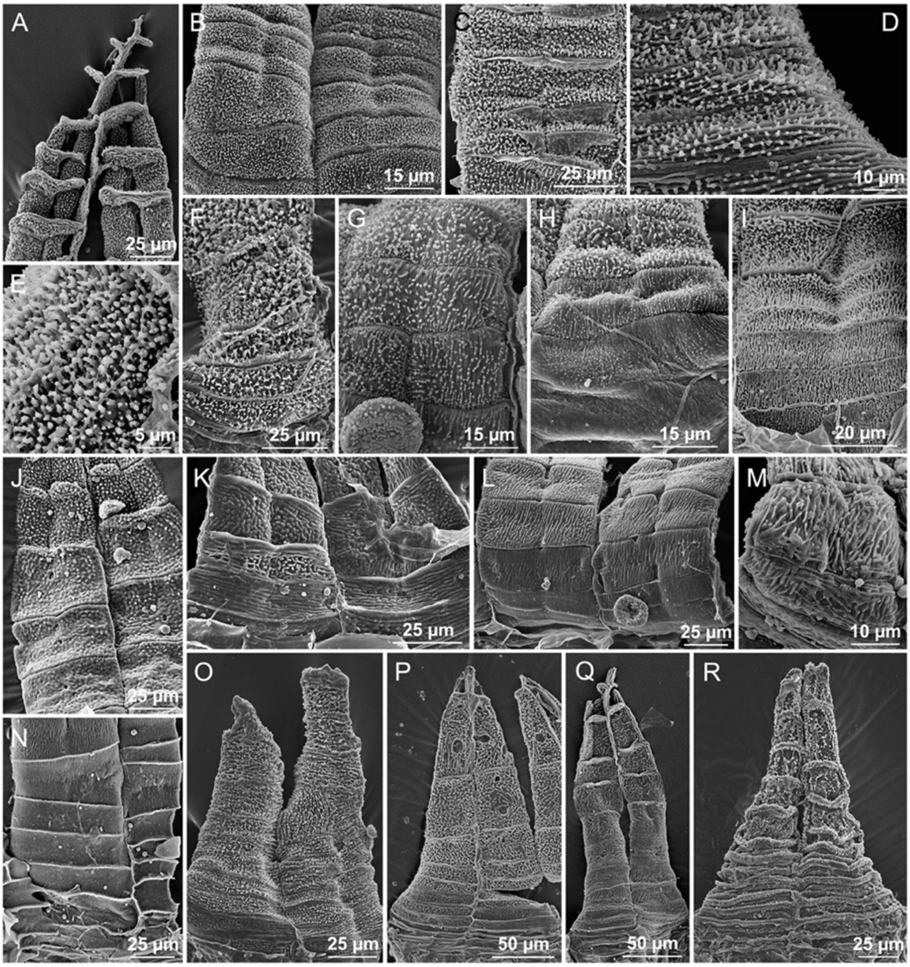


Fig. 17 – The inner surface of exostome teeth in some *Ulota* species. A, The upper part; B–I and K–N, The basal part; J, The middle part; O–R, The whole part. A, *U. robusta*; B, *U. cochleata*; C, *U. latisegmenta*; D, *U. coarctata*; E, *U. morrisonensis*; F, *U. drummondii*; G, *U. laticiliata*; H, *U. reptans*; I, *U. phyllantha*; J, *U. novo-guinensis*; K, *U. curvifolia*; L, *U. crispula*; M, *U. maltiana*; N, *U. obtusiuscula*; O, *U. coarctata*; P, *U. gigantospora*; Q, *U. megalospora*; R, *U. yakushimensis*. (all successively from *J. Kurz 2354* [non-type] in S, isotype in HO, holotype in PE, *J. Shaw 15435-1* [non-type] in DUKE, isotype in NICH, lectotype in E, lectotype in H, *Higuchi 41462* [non-type] in TNS, *W. B. Schofield 100736* [non-type] in DUKE, holotype in FH, *M. Sulayman K151* [non-type] in PE, *Y. Jia 09409* [non-type] in PE, *P. Dusén 434* [non-type] in H, *Vitt & Horton* [non-type] in FI, *W. B. Schofield 100736* [non-type] in DUKE, holotype in E, *W. B. Schofield & R. J. Belland no.84609* [non-type] in UBC and isotype in NUM).

and papillose above (figure 16O). In addition, the ornamentation on the inner surface of the teeth varies greatly from nearly smooth, striate to papillose (figure 17).

Preperistome is only common in one species within *Ulota*, *i.e. U. membranata* (figure 16M). It has been seen occasionally in a few other species, such as *Ulota crispa*, *U. curvifolia*, *U. fuegiana*, and *U. megalospora*. The ornamentation of preperistome is usually similar to that on the outer surface of the teeth.

Endostome segments

In *Ulota*, the number, shape, height, and ornamentation of endostome segments vary much greater than those of exostome teeth (figures 15 and 18), and they hence provide important criteria for the infrageneric classification. There are eight segments in most *Ulota* species, 16 (or eight long and eight short) in a few, such as *U. latisegmenta*, *U. membranata*, *U. morrisonensis*, and *U. novo-guinensis*, even less absent or rudimentary, including *U. coarctata*, *U. drummondii*, *U. perichaetialis*, *U. streptodon*, and *U. yakushimensis*. Some variations in the segment number exist in some species, such as *Ulota crispa*, whose segments are often eight, occasionally more, and even as many as 16.

Most segments are linear, linear-lanceolate, narrow-lanceolate, or lanceolate in shape; a few are wide-lanceolate, such as *Ulota billbuckii*, *U. magellanica*, *U. membranata*, and *U. robusta*, or filiform as in *U. cochleata*, *U. delicata*, and *U. fuegiana* (figure 15).

For the well-developed segments, they are almost always ≥2/3 height of the teeth (figure 15), variably incurved when dry. The basal membrane in all *Ulota* species is absent or inconspicuous, except *U. billbuckii*, *U. latisegmenta*, and *U. robusta* in which the basal membrane can be as high as 1/2 of the teeth.

Under the light microscope, in most endostome segments, the ornamentation on the inner surface is slightly scabrous, and a few are smooth or nearly so, such as *Ulota eurystoma* and *U. curvifolia*, or finely papillose as in *U. delicata* and *U. latisegmenta*, and only one is strongly and densely papillose, that is *U. macrodontia* (figure 15). The outer surface of all examined segments is smooth by SEM observations (figure 18). *Ulota macrodontia* was reported by Garilleti *et al.* (2021) to have strongly papillose ornamented in both surfaces but they failed to provide SEM image evidences.

Calyptra — This was once a key character in establishing the genus *Ulota* (Mohr, 1806), although later studies indicated that it is unreliable (Lewinsky, 1977). Calyptra in *Ulota* are all mitrate, but it varies in size, color, and hairiness (figure 19). In most *Ulota* species, the calyptra is moderate to strongly hairy. Although these hairs in some species have been described whether they have papillose or not, we have not seen any obvious difference and regularity among them. Besides, the hairs seem to grow randomly on the surface of the calyptra, except for *Ulota barclayi* whose hairs are only near the apex. There are also a few species with sparse hairs on the calyptra, such as *Ulota calvescens* and *U. magellanica*, and a few ones that are even naked, such as *U. macrocalycina* and *U. panchengiana*. Generally, the calyptra hairiness is stable in the same species, except for *Ulota fuegiana*, which has both moderately hairy calyptra and completely naked ones (figure 19). Moreover, the calyptra color seems to change irregularly and thus has no taxonomic value.

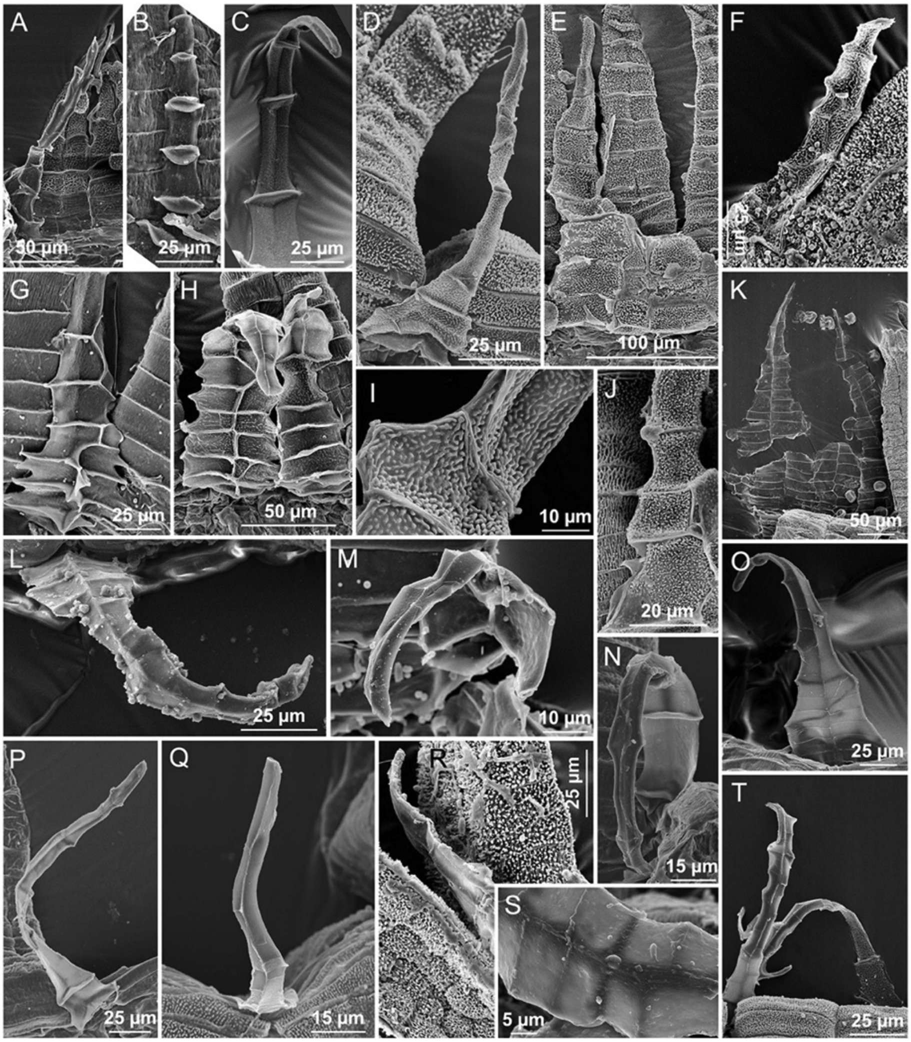


Fig. 18 – Endostome segments in some *Ulota* species. A–J, The inner surfaces; K–T, The outer surfaces. A, *U. curvifolia*; B, *U. eurystoma*; C, *U. japonica*; D, *U. fuegiana*; E, *U. latisegmenta*; F, *U. morrisonensis*; G, *U. obtusiuscula*; H, *U. magellanica*; I, *U. robusta*; J, *U. phyllantha*; K, *U. latisegmenta*; L, *U. splendida*; M, *U. yunnanensis*; N, *U. germana*; O, *U. japonica*; P, *U. megalospora*; Q, *U. macrocalycina*; R, *U. morrisonensis*; S, *U. magellanica*; T, *U. cochleata*. (all successively from *M. Sulayman K151* [non-type] in PE, isotype in KYO, holotype in FH, *T. Seki s.n.* [non-type] in H, holotype in PE, isotype in NICH, *Vitt & Horton* [non-type] in FI, *N. J. Andersson* [non-type] in S, isotype of *U. bellissima* in S, *W. B. Schofield 100736* [non-type] in DUKE, holotype in PE, holotype in FH, *L.-S. Wang 83-1173a* [non-type] in PE, *T. Seki no.2/32-61* [non-type] in H, holotype in FH, *D. H. Wagner m2525* [non-type] in DUKE, *C. J Cox no.319/00* [non-type] in DUKE, isotype in NICH, lectotype in PC and isotype in HO).

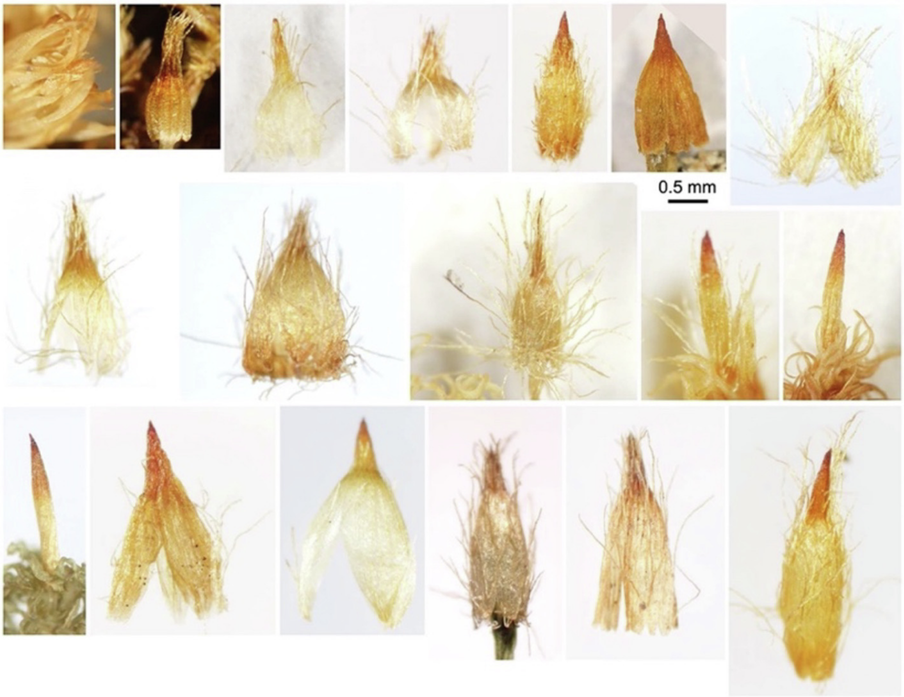


Fig. 19 – Calyptra diversity in *Ulota* species. The top line from left to right are: *U. perichaetialis*, *U. barclayi*, *U. phyllantha*, *U. curvifolia*, *U. novo-guinensis*, *U. macrocalycina*, *U. macrodontia*; the middle line from left to right: *U. obtusiuscula*, *U. gymnostoma*, *U. maltiana*, *U. fuegiana* (with hairs), *U. fuegiana* (naked); the bottom line from left to right are: *U. panchengiana*, *U. magellanica*, *U. calvescens*, *U. crispa*, *U. latisegmenta*, *U. splendida.* (all successively from lectotype in WELT, *W. B. Schofield 86158* [non-type] in DUKE, *W. B. Schofield 100736* [non-type] in DUKE, *Afonina s.n.* [non-type] in PE, holotype in FH, isotype in BM, lectotype in S [B157812], isotype in FH, *P.-C. Chen et al. 7047a* [non-type] in PE, *P. Dusén 434* [non-type] in S, isotype in E, isotype in E, holotype in PE, lectotype in PC, *L. Hedenäs* [non-type] in S, *S.-J. Li 116* [non-type] in PE, holotype in PE, holotype in FH).

The calyptra in all *Ulota* species cover the whole capsules or nearly so, only in *U. perbreviseta* and *U. perichaetialis* it covers only the upper part of capsules more or less (figure 19).

Spores — In most *Ulota* species, the spores are spherical, yellow, verrucose, and unicellular (figure 20). Most of these spores are 20–40 μm in diameter, only a few more than 40 μm, such as *Ulota magellanica* and *U. megalospora* (figure 21). Besides unicellular spores, multicellular spores are found in a few species of the genus *Ulota*. They are usually large, 60–130 μm in diameter (figure 21), spherical or irregularly shaped (figure 20). These species are all from Asia, Australasia, and South America, such as *Ulota membranata*, *U. novo-guinensis*, *U. streptodon*, and *U. yakushimensis*. In *Ulota*, the species with the smallest spores are *U. hutchinsiae* and *U. phyllantha*, while those with the largest spores are *U. novo-guinensis* and *U. streptodon* (figure 21). The smallest spore we have seen in this study is 10.9 μm in diameter from *Ulota hutchinsiae*, while the largest one is 140.4 μm in diameter from *U. novo-guinensis*.

Although the ornamentation on spore surfaces is difficult to see clearly under the light microscope (figure 20), some changes can be observed by SEM (figure 22). The papillose on the spore surfaces varies from small (*Ulota robusta* and *U. fuegiana*) to large (*U. drummondii* and *U. japonica*), from smooth (*U. ecklonii*, *U. rehmannii*, and *U. viridis*) to rough (*U. delicata* and *U. perichaetialis*). The surface ornamentation of multicellular spores is similar to that of unicellular spores (figure 22N–P) except for *Ulota novo-guinensis* and *U. yakushimensis*, of which the spores seem smooth, but it still needs to be confirmed by more materials.

It is worth noting that the spores in *Ulota eurystoma* were originally described as spherical and unicellular (Noguchi, 1939). However, all spores we have hitherto

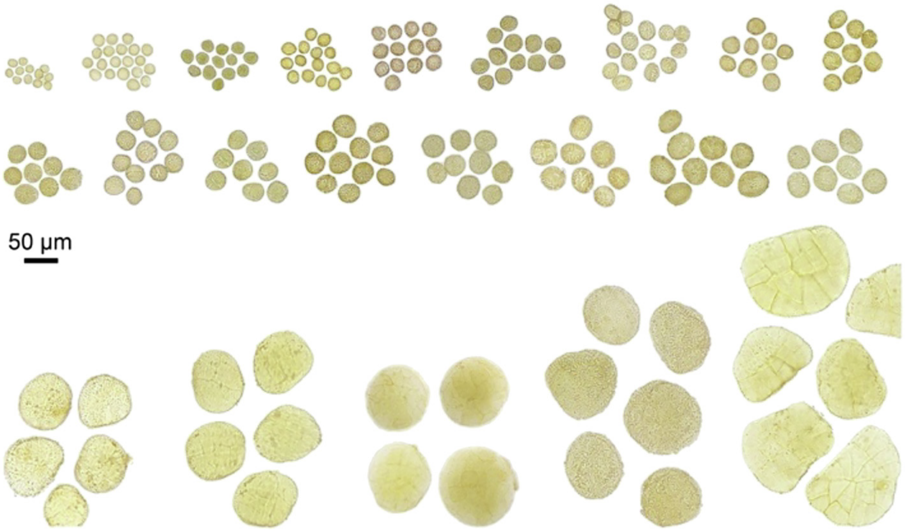


FIG. 20 – Spores in some *Ulota* species under light microscope. The top line from left to right are: *U. hutchinsiae*, *U. phyllantha*, *U. crispa*, *U. japonica*, *U. barclayi*, *U. fuegiana*, *U. coarctata*, *U. rehmannii* and *U. ecklonii*; the middle line from left to right are: *U. maltiana*, *U. cochleata*, *U. gymnostoma*, *U. delicata*, *U. viridis*, *U. splendida*, *U. megalospora* and *U. magellanica*; the bottom line from left to right are: *U. yunnanensis*, *U. membranata*, *U. yakushimensis*, *U. billbuckii* and *U. streptodon*. (all successively from *R. R. Ireland 15528* [non-type] in UBC, *W. B. Schofield 100736* [non-type] in DUKE, *S.-J. Li 116* [non-type] in PE, holotype in FH, isotype in FH, *J. F. Engel* [non-type] in H, *M. Dickron* [non-type] in BM, *h3227* [non-type] in BP, isotype in S, *P. Dusén 434* [non-type] in S, isotype in HO, *P.-C. Chen 7047a* [non-type] in PE, holotype in PE, *G. O. K. Sainsbury* [non-type] in S, *T. Koponen 32460* [non-type] in S, *W. B. Schofield & J. H. Lyford 72252* [non-type] in UBC, *R. R. Ireland & G. Bellolio 36077* [non-type] in MO, holotype in E, *L. Vish 113* [non-type] in H, holotype in NICH, *C. J. Cox no.595/00(2)* [non-type] in DUKE, *A. Hollermager 1668* [non-type] in PC).

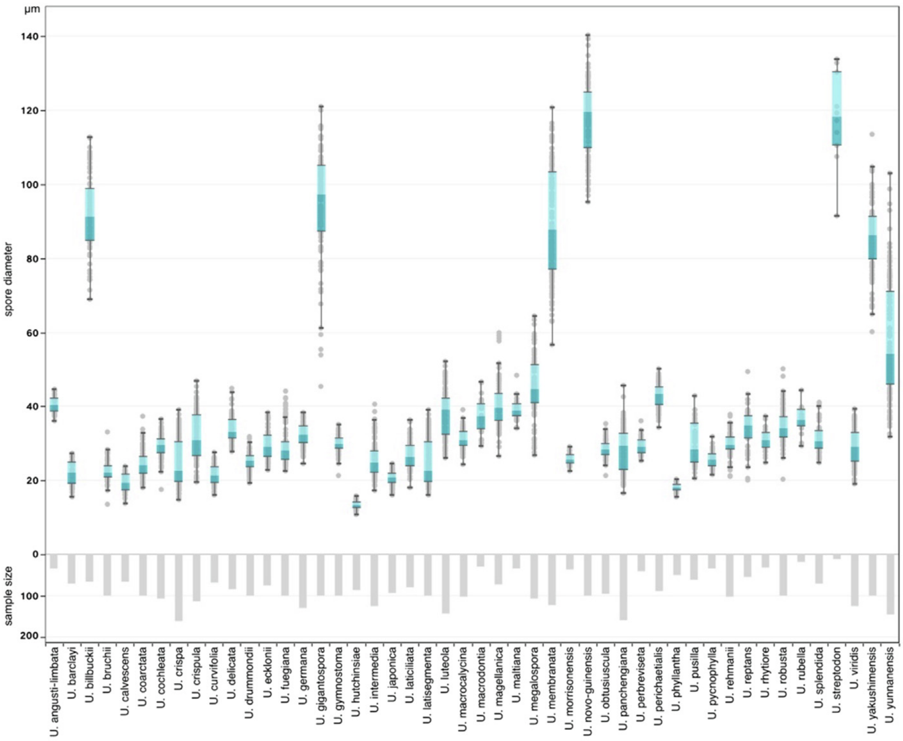


Fig. 21 – Spore diameters in *Ulota* species. The gray bars represent sample size for each species.

observed in this species have pregerminated with long protonema, multicellular and irregular in shape. Therefore, the spore morphology in *Ulota eurystoma* needs to be confirmed with more specimens.

Spores size is an adaptive trait wherein small spores have a good chance for long-distance dispersal, and large spores do not, especially multicellular spores, but have a greater chance for successful germination and establishment (Kürschner and Parolly, 1998). Few bryophytes are able to use both strategies, including *Leptodontium viticulosoides* (P. Beauv.) Wijk & Margad. from Andes of northern Peru and *Macromitrium erythrocomum* H.P. Ramsay, A. Cairns & Meagher from the Australian Tropics (Ramsay *et al.*, 2017).

4.2 Taxa

Ulota Mohr. Ann. Bot. 2: 540. 1806. ≡ *Orthotrichum* sect. *Ulota* (Mohr) Müll. Hal., Syn. Musc. Frond. 1: 711. 1849. ≡ *Orthotrichum* subgen. *Ulota* (Mohr) Boulay, Musc. France, Mousses 342. 1884. Type: *U. crispa* (Hedw.) Brid., (lectotype, designated by Vitt, 1970).

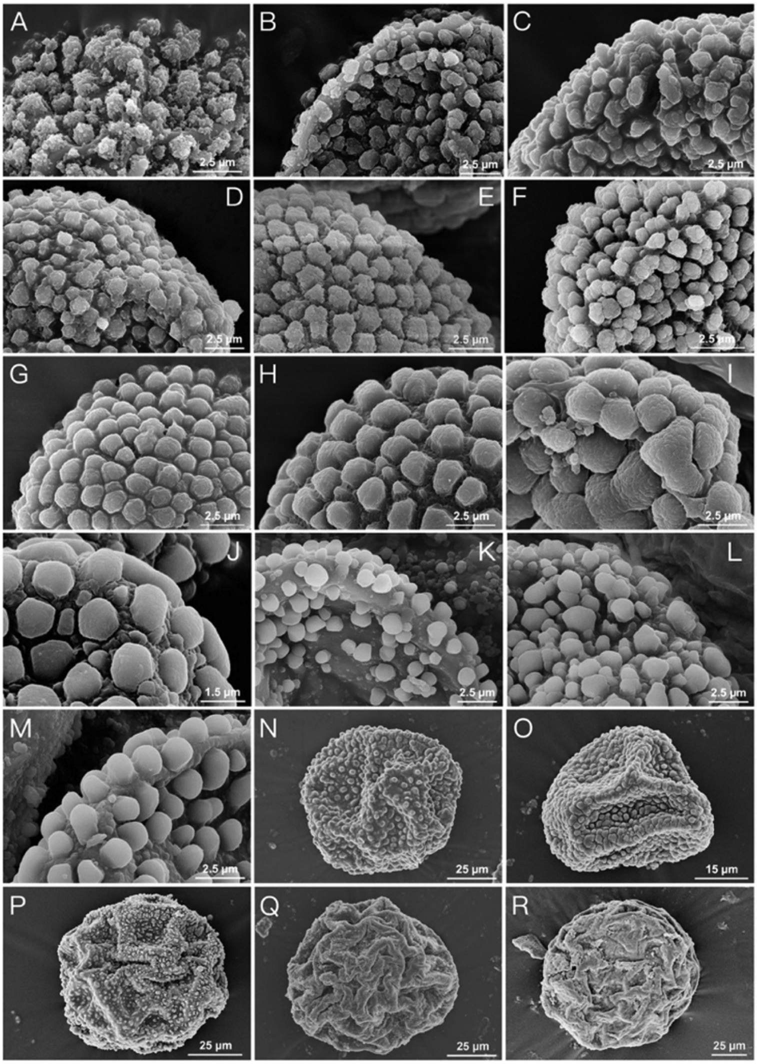


FIG. 22 – The ornamentation on spore surface in some *Ulota* species. A, *U. perichaetialis*; B, *U. robusta*; C, *U. fuegiana*; D, *U. laticiliata*; E, *U. delicata*; F, *U. morrisonensis*; G, *U. latisegmenta*; H, *U. curvifolia*; I, *U. drummondii*; J, *U. japonica*; K, *U. viridis*; L, *U. ecklonii*; M, *U. rehmannii*; N, *U. gigantospora*; O, *U. yunnanensis*; P, *U. membranata*; Q, *U. yakushimensis*; R, *U. novo-guinensis.* (all successively from lectotype in WELT, isotype of *U. bellissima* in S, *T. Seki s.n.* [non-type] in H, lectotype in H, *Q. Gao* [non-type] in IFP, isotype in NICH, holotype in PE, *M. Sulayman K151* [non-type] in PE, lectotype in E, holotype in FH, isotype in H, isotype in S, *J. Breiveer* [non-type] in HBG, holotype in E, *L.-S. Wang 83-1173a* [non-type] in PE, *G. O. K. Sainsbury 348* [non-type] in S, isotype in NUM and holotype in FH).

Weissia Ehrh. ex G. Gaertn., B. Mey. & Scherb., Oekon. Fl. Wetterau 3(2): 94. 1802.
Illegitimate, later homonym.
Bryodixonia Sainsbury, Trans. & Proc. Roy. Soc. New Zealand 75: 177. 1945.

Plants green to dark, 0.5–3 (–9) cm high, in tufts or cushions. Leaves are usually crisped when dry, sometimes erect to flexuose, wide-spreading to patent when moist, lanceolate from a broader base, acuminate to long acuminate at apexes. Costa single and strong, ending near the apex. Upper and middle laminal cells rounded, hexagonal or oblong, thick-walled, mostly with low or high papillae; basal inner cells rectangular, elongate-rectangular or vermiculate, smooth, strongly or rarely slightly thick-walled; basal margin differentiated in (1–) 3–10 (–15) rows hyaline cells, quadrate to rectangular, with thickened transverse walls, sometimes equally thickened both transversal and longitudinal walls.

Autoicous, rarely dioicous. Perichaetial leaves are often slightly differentiated, rarely remarkably longer. Capsules short or long exserted, seldom emergent or immersed, short- to long-cylindrical, rarely obovoid, pyriform, fusiform, or subglobose, mostly 8-ribbed, variably constricted when dry. Stomata superficial, confined to the urn or the junction between the urn and neck. Preperistome is rarely present. Peristome double, rarely single or absent; exostome teeth 16, often united into 8 pairs, lanceolate, reflexed or recurved, rarely erect-spreading or incurved when dry, papillose or striate; endostome segments 8, rarely 16, rudimentary or absent, linear to narrow-lanceolate, rarely filiform or wide-lanceolate, hyaline or pale yellow, rarely dark yellow, smooth outside, slightly to strongly coarse inside. Opercula with a short or long rostrum. Calyptra mitrate, variably hairy, seldom naked. Spores unicellular, globose, rarely multicellular with irregularly shaped, finely papillose to verrucose, 17–40 μm in diameter, often more than 100 μm when multicellular.

Notes: The genus *Ulota* is easy to be recognized, including most plants small in size, often crisped leaves when dry, more or less hyaline cells at leaf marginal bases with thickened transverse walls, most exserted and cylindrical capsules that often constrict with varying degrees when dry and empty, and mitrate calyptra usually with hairs.

Ulota is closely related to *Orthotrichum* s.l., which has recently been divided into four genera, including *Lewinskya*, *Nyholmiella*, *Orthotrichum*, and *Pulvigera* (Garilleti *et al.*, 2021; Lara *et al.*, 2016; Plášek *et al.*, 2015). Among them, *Lewinskya* is the closest one to *Ulota*, and they share mainly in the phenotypic stomata. However, *Lewinskya* differs in the non-crisped leaves and undifferentiated cells at leaf marginal bases.

In the field, *Ulota* is easy to be confused with *Ptychomitrium* Fürnr. They both have crisped leaves, exserted and cylindrical capsules, but *Ptychomitrium* can be distinguished by the smooth capsule or nearly so when dry, single peristome that often erect-spreading when dry, always naked calyptra and exclusively saxicolous habitats, as well as other differences under a microscope.

In *Ulota*, the morphological variation is much greater in sporophytes than in gametophytes, and therefore capsules are indispensable and essential for species determination. The main characters for infrageneric classification contain the dry state of leaves, differentiation degree of leaf basal marginal cells, capsule shape and its dry state, seta length, peristome configuration, stoma position, spore size, and calyptra hairiness.

4.2.1 Recognized Species

Keys are provided for the identification of species in *Ulota* from six continents.

Key to Taxa of *Ulota* in Asia

1. Plants dioicous; gammae common, cylindrical, reddish, on the apex of leaves at the top of branches or stems; capsules rarely present; restricted to maritime habitats........**38. *U. phyllantha***
1. Plants autoicous; gammae never or hardly produced; capsules often present; not confined to maritime habitats........2
2. Peristome absent or sometimes rudimentary; capsules fusiform, oblong-cylindrical or elliptical when dry and empty........**18. *U. gymnostoma***
2. Peristome present and well-developed; capsules cylindrical, rarely obovoid or subglobose........3
3. Stomata on the urn, usually central and upper part; calyptra always naked........**35. *U. panchengiana***
3. Stomata confined to the base of urn or the transition zone between urn and neck; calyptra more or less hairy, rarely naked........4
4. Peristome single; leaves erect to variably flexuose but not crisped when dry........5
4. Peristome double; leaves erect, flexuose or variably crisped when dry........6
5. Capsules long-cylindrical, strongly constricted when dry, often with somewhat puckered mouth; spores small, unicellular........**12. *U. drummondii***
5. Capsules subglobose, not or hardly constricted when dry, with no or slightly puckered mouth; spores large, multicellular........**49. *U. yakushimensis***
6. Leaves erect-appressed when dry; spores smaller, 13–14 μm...**19. *U. hutchinsiae***
6. Leaves flexuose to variably crisped when dry; spores relatively large, 19–105 μm........7
7. Spores multicellular, large, 46–105 μm; leaf cells at basal margins weakly differentiated, ≤4 rows of hyaline cells........8
7. Spores unicellular, small, 19–38 μm; leaf cells at basal margins usually distinctly differentiated, ≥4 rows of hyaline cells........9
8. Exostome teeth with densely papillose and often cancellate at the upper part; calyptra moderately hairy; spores relatively large, 87–105 μm................**17. *U. gigantospora***
8. Exostome teeth with prominent striate and almost never cancellate at the upper part; calyptra naked to sparsely hairy; spores small, 46–71 μm................**50. *U. yunnanensis***
9. Exostome teeth weakly ornamentated with wrinkle to striolate; capsules obovoid or funnel-shaped, not or slightly constricted when dry and empty........**14. *U. eurystoma***
9. Exostome teeth moderately to strongly ornamentated with papillose and striate; capsules cylindrical, sometimes funnel-shaped, often strongly, sometimes slightly constricted below the mouth when dry and empty........10
10. Exostome teeth strongly striate........11
10. Exostome teeth densely papillose or papillose-striate........12

11. Leaf cells at basal margins weakly differentiated into 1–4 rows of hyaline cells; middle and upper leaf cells with prominent conic or forked papillae; calyptra moderately to strongly hairy; spores small, 19–24 μm; mostly grows on rocks........**10. *U. curvifolia***
11. Leaf cells at basal margins distinctly differentiated in 4–6 rows of hyaline cells; middle and upper leaf cells smooth or with low papillose; calyptra sparsely hairy to naked; spores relatively large, 28–32 μm; always grow on trees........**41. *U. rehmannii***
12. Endostome segments wide, lanceolate; leaf cells at basal leaf margins differentiated into 2–4 rows of hyaline cells........13
12. Endostome segments narrow, linear, narrow-lanceolate; leaf cells at basal leaf margins often differentiated into 3–11 rows, rarely 1–2 rows of hyaline cells........14
13. Endostome segments finely papillose; capsules often strongly constricted; plants smaller, 1–2 cm; spores smaller, 19–25 μm........**24. *U. latisegmenta***
13. Endostome segments striate; capsules hardly constricted; plants larger, 1–4 cm; spores larger, 32–37 μm........**44. *U. robusta***
14. Endostome segments filiform, fragile; capsules with puckered mouth when dry........**11. *U. delicata***
14. Endostome segments linear, narrow-lanceolate or linear-lanceolate; capsules without puckered mouth when dry........15
15. Leaves short, 1.3–1.6 mm; leaf cells at basal margins weakly differentiated, no more than three rows of hyaline cells........**42. *U. reptans***
15. Leaves relatively long, 1.7–4.1 mm; leaf cells at basal margins distinctly differentiated, 3–11 rows of hyaline cells........16
16. Capsules fully emergent, short-cylindrical........**36. *U. perbreviseta***
16. Capsules short or long exserted, cylindrical, sometimes short-cylindrical........17
17. Endostome segments 16, finely papillose inside; leaves longer, 2.5–4.1 mm; leaf cells at basal margins differentiated in less rows (3–6); seta longer, 5.3–7 mm........**32. *U. morrisonensis***
17. Endostome segments 8, rarely up to 16, slightly scabrous or finely papillose or nearly smooth inside; leaves relatively shorter, 1.7–3 mm; leaf cells at basal margins often differentiated in more rows (4–11); seta relatively shorter, 2–5 mm........18
18. Capsules moderately to strongly constricted below mouth when dry and empty........19
18. Capsules slightly, sometimes moderately constricted below the mouth when dry........20
19. Leaves strongly crisped when dry, with distinctly wide base; leaf basal inner cells with strongly thickened wall; plants large, 0.5–2.5 cm; calyptra densely hairy........**8. *U. crispa***
19. Leaves often flexuose when dry, with slightly wide base; leaf basal inner cells with slightly to moderately thickened wall; plants small, 0.5–1 cm; calyptra sparsely hairy or naked........**21. *U. japonica***

20. Leaves flexuous, slightly to moderately crisped when dry; endostome segments linear, slender and fragile, often with thin cross-walls on the inside ....**9. *U. crispula***
20. Leaves strongly crisped when dry; endostome segments linear to linear-lanceolate, not fragile, often with distinctly thickened and prominent cross-walls on the inside..**20. *U. intermedia***

KEY TO TAXA OF *ULOTA* IN OCEANIA

1. Plants dioicous; gammae common, cylindrical, reddish, on the apex of leaves at the top of branches or stems; capsules rarely present; restricted to maritime habitats...**38. *U. phyllantha***
1. Plants autoicous; gammae never or hardly produced; capsules often present; not confined to maritime habitats...2
2. Capsules immersed; peristome single; perichaetial leaves extremely longer; calyptra small, covering only the upper part of capsules................ ....**37. *U. perichaetialis***
2. Capsules emergent to exserted; peristome double; perichaetial leaves somewhat to much longer; calyptra large, covering the whole capsules or nearly so.................3
3. Spores multicellular, large, 84–125 μm; endostome segments 16..........................4
3. Spores unicellular, small, 19–42 μm; endostome segments 8, rarely up to 16........5
4. Leaves erect or flexuose when dry; leaf cells at basal margins distinctly differentiated into 4–6 rows; capsules obovoid, ovate-cylindrical or short-cylindrical when dry; endostome segments wide, lanceolate to wide-lanceolate; spores comparatively small, 84–105 μm...**31. *U. membranata***
4. Leaves strongly crisped when dry; leaf cells at basal margins weakly differentiated, only one, rarely two rows; capsules cylindrical to short-cylindrical when dry; endostome segments narrow, linear; spores large, 110–125 μm......................... ....**33. *U. novo-guinensis***
5. Leaves erect or flexuose when dry...**48. *U. viridis***
5. Leaves strongly crisped when dry...6
6. Plant large, 2–3 cm, sometimes up to 9 cm; leaves narrow-lanceolate; opercula with a long beak...**46. *U. splendida***
6. Plant relatively small, 0.5–2.5 cm; leaves lanceolate; opercula with a short, rarely long beak...7
7. Leaf cells at basal margins weakly differentiated, no more than three rows of hyaline cells; endostome segments smooth inside; spores relatively large, 35–42 μm..8
7. Leaf cells at basal margins distinctly differentiated, 4–11 rows of hyaline cells; endostome segments papillose or variously coarse, rarely nearly smooth inside; spores small, 19–31 μm..9
8. Capsules cylindrical, 1.8–2.5 mm long, strongly constricted when dry; leaves longer, 2.7–2.9 mm; calyptra sparsely hairy.................................**45. *U. rubella***
8. Capsules short-cylindrical, ca. 1 mm long, more or less constricted when dry; leaves shorter, 2.2–2.4 mm; calyptra densely hairy............**1. *U. angusti-limbata***

9. Stomata at the central and lower part of urn; endostome segments filiform to linear, often fragile; capsules not or slightly constricted when dry and empty..**7. *U. cochleata***
9. Stomata at the junction between urn and neck; endostome segments narrow-lanceolate to lanceolate; capsules moderately to strongly constricted when dry and empty..10
10. Endostome segments narrow-lanceolate, 1/2–1/4 width of teeth in the middle; plants relatively large, 0.5–2.5 cm high; capsules relatively large, 1.4–2.2 mm long..**8. *U. crispa***
10. Endostome segments lanceolate, about 1/2 width of teeth in the middle; plants small, 0.6–1.3 cm high; capsules small, 1.2–1.5 mm long..........**23. *U. laticiliata***

KEY TO TAXA OF *ULOTA* IN EUROPE

1. Plants dioicous; gammae common, cylindrical, reddish, on the apex of leaves at the top of branches or stems; capsules rarely present; restricted to maritime habitats..**38. *U. phyllantha***
1. Plants autoicous; gammae never or hardly produced; capsules often present; not confined to maritime habitats..2
2. Peristome single; capsules with puckered mouth when dry; leaves erect to flexuose when dry...3
2. Peristome double; capsules without puckered mouth when dry; leaves crisped, sometimes erect or flexuose when dry..4
3. Capsules pyriform, only strongly constricted at mouth when dry; leaf cells at basal margins weakly differentiated, 2–4 rows of hyaline cells...**6. *U. coarctata***
3. Capsules long cylindrical, distinctly constricted below mouth when dry; leaf cells at basal margins distinctly differentiated, 4–6 rows of hyaline cells..**12. *U. drummondii***
4. Leaves erect-appressed when dry; leaf cells at basal margins not differentiated or weakly differentiated into no more than 3 rows of hyaline cells; spores smaller, 13–14 μm..**19. *U. hutchinsiae***
4. Leaves flexuose to crisped, rarely erect when dry; leaf cells at basal margins often differentiated into 3–11 rows of hyaline cells; spores relatively large, 17–38 μm...5
5. Exostome teeth strongly striate; leaves erect to variably flexuose, rarely crisped when dry..6
5. Exostome teeth densely papillose or papillose-striate; leaves crisped, sometimes flexuose when dry..7
6. Leaf cells at basal margins weakly differentiated into 1–4 rows of hyaline cells; middle and upper leaf cells with prominent conic or forked papillae; calyptra moderately to strongly hairy; spores relatively small, 19–24 μm; mostly grows on rocks...**10. *U. curvifolia***
6. Leaf cells at basal margins distinctly differentiated in 4–6 rows of hyaline cells; middle and upper leaf cells smooth or with low papillose; calyptra sparsely hairy to naked; spores large, 28–32 μm; always grow on trees..........**41. *U. rehmannii***

7. Leaves with often 3–4 rows elongate cells inside the margin, ascending above the base, usually up to central part; calyptra often sparsely hairy; spores small, 17–22 µm..........**5. *U. calvescens***

7. Leaves without elongate cells inside the margin; calyptra densely hairy; spores comparatively large, 19–38 µm..........8

8. Capsules with distinctly long neck when empty and dry; endostome segments striate at lower part..........**4. *U. bruchii***

8. Capsules with short neck when empty and dry; endostome segments slightly scabrous to nearly smooth..........9

9. Capsules moderately to strongly constricted below the mouth when dry and empty; exostome teeth often bordered by a hyaline halo..........**8. *U. crispa***

9. Capsules often hardly or slightly constricted below the mouth when dry and empty; exostome teeth never bordered by a hyaline halo..........10

10. Leaves flexuous, slightly to moderately crisped when dry; endostome segments linear, slender and fragile, often with thin cross-walls on the inside..........**9. *U. crispula***

10. Leaves strongly crisped when dry; endostome segments linear to linear-lanceolate, not fragile, often with distinctly thickened and prominent cross-walls on the inside..........**20. *U. intermedia***

Key to Taxa of *Ulota* in Africa and surrounding islands

1. Leaves with often 3–4 rows elongate cells inside the margin, ascending above the base, usually up to central part; calyptra often sparsely hairy; spores small, 17–22 µm..........**5. *U. calvescens***

1. Leaves without elongate cells inside the margin; calyptra densely hairy; spores comparatively large, 19–32 µm..........3

2. Stomata on the junction between urn and neck; seta longer, 3–5 mm; spores small, 19–25 µm..........**8. *U. crispa***

2. Stomata on the central or lower part of urn, sometimes on the junction between urn and neck; seta shorter, 1.7–2.9 mm; spores larger, 26–32 µm..........**13. *U. ecklonii***

Key to Taxa of *Ulota* in North America

1. Plants dioicous; gammae common, cylindrical, reddish, on the apex of leaves at the top of branches or stems; capsules rarely present; restricted to maritime habitats..........**38. *U. phyllantha***

1. Plants autoicous; gammae never or hardly produced; capsules often present; not confined to maritime habitats..........2

2. Peristome absent; capsules emergent, fusiform, oblong-cylindrical or elliptical when dry, with puckered mouth; stomata scattered on the urn;..........**43. *U. rhytiore***

2. Peristome present; capsules exserted or rarely fully emergent, cylindrical or rarely pyriform when dry, occasionally with puckered mouth; stomata on transition between urn and neck, seldom on the urn..........3

3. Endostome segments absent or rudimentary; capsules with puckered mouth when dry........4
3. Endostome segments well-developed; capsules without puckered mouth when dry........5
4. Capsules pyriform, only strongly constricted at mouth when dry; leaf cells at basal margins weakly differentiated, 2–4 rows of hyaline cells........***6. U. coarctata***
4. Capsules long cylindrical, distinctly constricted below mouth when dry; leaf cells at basal margins distinctly differentiated, 4–6 rows of hyaline cells........***12. U. drummondii***
5. Leaves erect-appressed, slightly flexuose when dry........6
5. Leaves variably flexuose to strongly crisped when dry........7
6. Leaf cells at basal margins not differentiated or weakly differentiated into no more than 3 rows of hyaline cells; calyptra densely hairy; spores smaller, 13–14 μm; grows on rocks, rarely on trees........***19. U. hutchinsiae***
6. Leaf cells at basal margins often differentiated into 5–12 rows of hyaline thin-walled cells; calyptra sparsely hairy near the apex, rarely naked; spores relatively large, 19–25 μm; grows on trees........***2. U. barclayi***
7. Leaves variably flexuose to weakly crisped when dry; leaf cells at basal margins weakly differentiated into 1–4 rows of hyaline cells........8
7. Leaves strongly crisped when dry; leaf cells at basal margins distinctly differentiated, 3–11 rows of hyaline cells........9
8. Plant 2–3 cm tall; leaves relatively long, 1.6–2.2 mm; middle and upper leaf cells with prominent conic or forked papillae; calyptra moderately to strongly hairy; spores small, 19–24 μm; grows on rocks, rarely on trees........***10. U. curvifolia***
8. Plant less than 1 cm tall; leaves short, 1.2–1.7 mm; middle and upper leaf cells with low papillae; calyptra sparsely hairy; spores large, 41–51 μm; grows only on trees........***30. U. megalospora***
9. Capsules moderately to strongly constricted when dry and empty........***8. U. crispa***
9. Capsules hardly or slightly constricted below the mouth when dry and empty........10
10. Capsules never becoming red or orange near mouth; seta relatively short, 2.5–4 mm; plant relatively small, 1–1.5 cm; leaves relatively short, 2.4–3.0 mm; endostome segments linear to linear-lanceolate........***20. U. intermedia***
10. Capsules often becoming red or orange near mouth; seta long, 5–7.5 mm; plant large, 1–3.5 cm; leaves longer, 2.8–3.7 mm; endostome segments narrow-lanceolate........***34. U. obtusiuscula***

KEY TO TAXA OF *ULOTA* IN SOUTH AMERICA

1. Plants dioicous; gammae common, cylindrical, reddish, on the apex of leaves at the top of branches or stems; capsules rarely present; restricted to maritime habitats........***38. U. phyllantha***
1. Plants autoicous; gammae never or hardly produced; capsules often present; not confined to maritime habitats........2

2. Spores multicellular, large, 85–140 μm..3
2. Spores unicellular, relatively small, 19–44 μm..5
3. Leaves narrow-lanceolate, often sinuose upper part, with ovate base; capsules somewhat puckered at mouth when dry and empty; endostome segments absent, sometimes rudimentary..***47. U. streptodon***
3. Leaves lanceolate, not sinuose upper part, with round base; capsules never puckered at mouth when dry and empty; endostome segments well-developed 4
4. Endostome segments remarkably connected by some cells at lower half part..***3. U. billbuckii***
4. Endostome segments almost free at the base..............................***22. U. larrainii***
5. Leaves cells at basal margins weakly differentiated, no more than three rows..6
5. Leaves cells at basal margins distinctly differentiated into 4–11 rows..7
6. Endostome segments 16, wide-lanceolate; calyptra sparsely hairy to naked; vaginula strongly hairy; spores relatively large, 36–44 μm.................. ....***28. U. magellanica***
6. Endostome segments 8, linear to narrow-lanceolate; calyptra densely hairy; vaginula naked or rarely hairy; spores small, 29–34 μm..................***25. U. luteola***
7. Endostome segments strongly ornamentated as much as exostome teeth, dark yellow..***27. U. macrodontia***
7. Endostome segments finely ornamentated to smooth, yellowish, or hyaline 8
8. Leaves erect-appressed to slightly flexuose when dry; leaves short, 1.1–1.5 mm, with ovate to oblong bases; hyaline leaf cells at basal margins with thin walls..9
8. Leaves flexuose to strongly crisped when dry; leaves longer, 1.3–2.9 mm, with rounded bases; hyaline leaf cells at basal margins with only thickened transverse walls, sometimes with thin walls..10
9. Leaf apex acute; stomata often on the urn; calyptra always naked; exostome teeth with densely papillose inside; spores relatively larger, 29–33 μm ....***26. U. macrocalycina***
9. Leaf apex often acuminate; stomata on the transition zone between urn and neck; calyptra densely hairy; exostome teeth with papillose-striate inside; spores small, 24–27 μm..***40. U. pycnophylla***
10. Leaves flexuose, sometimes crisped when dry; capsules hardly or slightly constricted below the mouth; stomata scattered on the urn...................................11
10. Leaves strongly crisped when dry; capsules moderately to strongly constricted below the mouth; stomata on the urn or at the junction between urn and neck..12
11. Endostome segments 8, filiform, fragile; leaves relatively longer, 1.8–2.4 mm; hyaline leaf cells at basal margins with only transversely thickened walls...***15. U. fuegiana***

11. Endostome segments 16, linear to narrow-lanceolate; leaves short, 1.3–1.5 mm; hyaline leaf cells at basal margins with thin or rarely transversely thickened walls............**39. *U. pusilla***
12. Endostome segments 16, smooth inside; stomata on the central or lower part of urn; spores comparatively large, 37–41 μm............**29. *U. maltiana***
12. Endostome segments 8, rarely up to 16, slightly scabrous to nearly smooth inside; stomata at the lower part of urn or the junction between urn and neck; spores small, 19–35 μm............13
13. Perichaetial leaves shorter, 1.8–2.9 mm, not prominently sheathing the seta; seta longer, 3–5 mm; capsules longer, 1.4–2.2 mm; spores relatively smaller, 19–25 μm............**8. *U. crispa***
13. Perichaetial leaves longer, 2.8–3.4 mm, often prominently sheathing the seta; seta shorter, 1.7–2.9 mm; capsules shorter, 1–1.2 mm; spores large, 32–35 μm............**16. *U. germana***

1. **ULOTA ANGUSTI-LIMBATA** E.B. Bartram, Bryologist 48: 116. 1945. TYPE: PAPUA NEW GUINEA. Rawlinson Range, alt. 7000–12000 ft., 22 Jul. 1941, *Clemens no. 12445B. 1.* (holotype, FH00079853–54! isotype, MICH!)

Plants 0.5–2 cm tall, yellowish green to green above, brown to black below. Stems usually branched. Leaves strongly crisped when dry, patent when moist, (2–) 2.2–2.4 (–2.5) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex long acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, (6–) 9–11 (–14) × (7–) 9–11 (–13) μm, thick-walled, often with low simple papillae; basal inner cells linear, rectangular to elongate- rectangular, (21–) 28–39 (–54) × (1–) 2–6 (–8) μm, with strongly thickened wall, smooth; basal marginal cells weakly differentiated, 1–3 rows, rarely up to 5 rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves are somewhat longer, ca. 2.9 mm. Vaginula unknown. Seta 7–7.3 mm long, twisted anticlockwise when dry. Capsule long exserted, ca. 1 mm long. Urn short-cylindrical, more or less constricted below the mouth when dry and empty, eight furrows along the entire length, with prominent ribs alternately yellow. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, four to five cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the transition zone between urn and neck. Preperistome rarely present. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved and lying on the exothecium when dry, lanceolate, densely and finely papillose on the outside, striate on the inside. Endostome segments 8, linear-lanceolate, almost reaching the exostome teeth, uniseriate upper, irregularly biseriate at the base, hyaline, variably incurved when dry, smooth on both surfaces. Opercula with a short beak. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (36–) 38–42 (–45) μm in diameter.

Illustration: Vitt *et al.* (1993); figures 23–25.

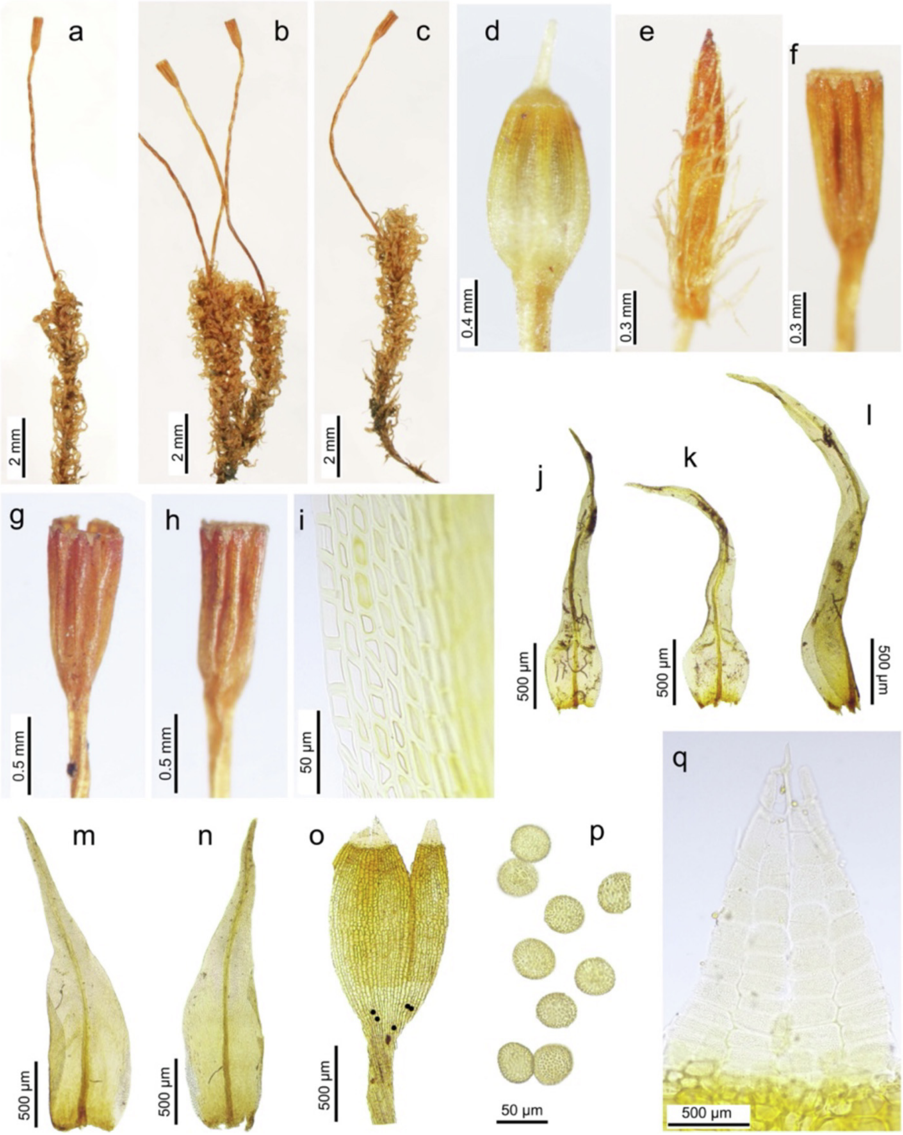


FIG. 23 – *Ulota angusti-limbata* E.B. Bartram. a–c. Habit. d. A capsule with an operculum. e. Calyptra. f–h. Capsules in dry and empty. i. Marginal cells at leaf base. j and k. Leaves. l. Outer perichaetial leaves. m and n. Inner perichaetial leaves. o. Exothecial wall, with dots indicating stoma position. p. Spores. q. Peristome, with endostome segments caducous. (a–c, e–l, o and q from holotype [FH], d from *A. Touw 16274* [non-type, S], m, n and p from *D. H. Norris 62727B* [non-type, H]).

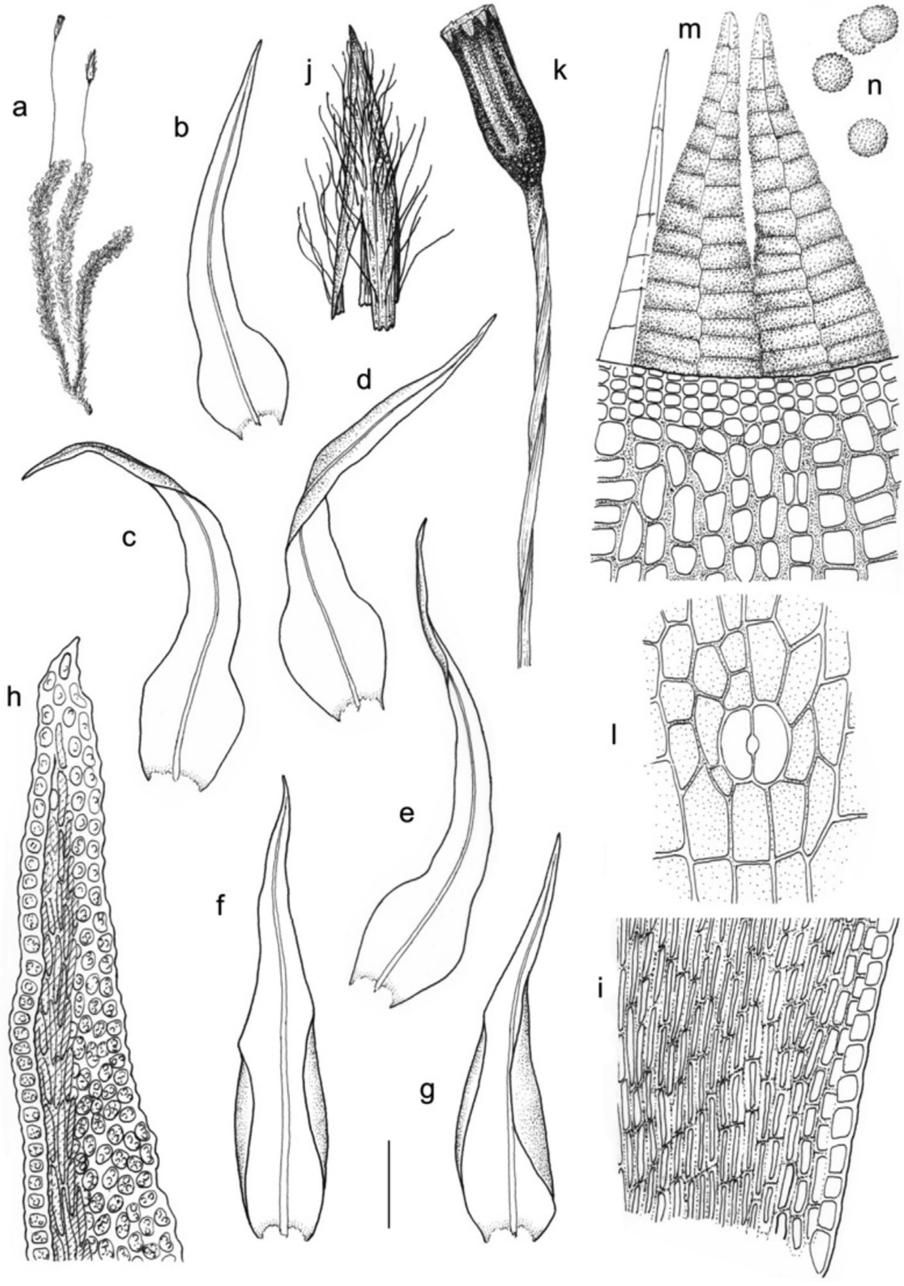


FIG. 24 – *Ulota angusti-limbata* E.B. Bartram. a. plant; b–e. leaves; f–g. perichaetial leaves; h. top laminal cells; i. basal marginal cells; j. calyptra; k. an empty capsule in dry; l. stoma; m. a portion of peristome; n. spores. (Scale bar: a, 5 mm; b–g, k, j, 0.5 mm; h, i, m, 0.05 mm; l, 0.04 mm; n, 0.07 mm. All drawn from holotype in FH).

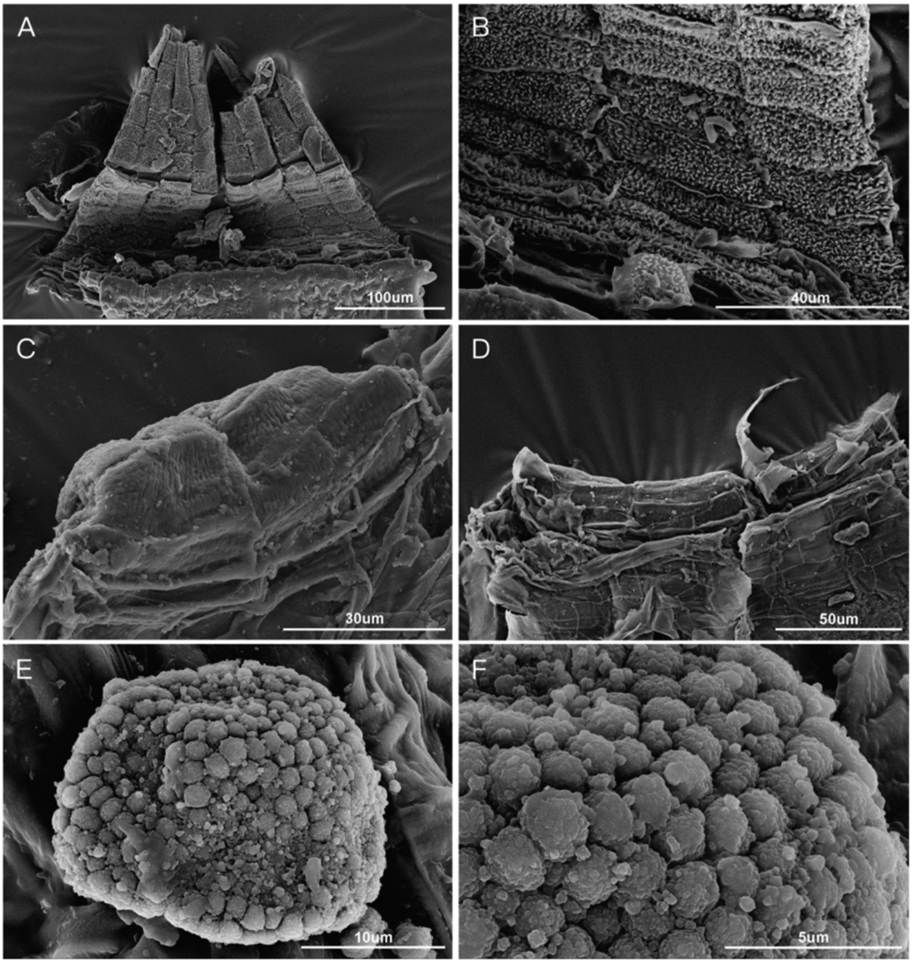


FIG. 25 – *Ulota angusti-limbata* E.B. Bartram. A, outer surface of upper exostome; B, outer surface of basal exostome; C, inner surface of basal exostome; D, endostome; E, a spore; F, surface ornamentation of a spore. (All from the holotype in FH).

Habitat: It grows on branches or trunks of trees or shrubs, only recorded on *Rhododendron*. There are some records of altitude: 3300–3500 m.

Distribution: It is **endemic** to Papua New Guinea. Figure 26.

Notes: The prominent features of *Ulota angusti-limbata* are weakly differentiated leaf basal marginal cells, very long seta, and short capsules. The endostome segments of *Ulota angusti-limbata* were considered rudimentary (Vitt *et al.*, 1993), but according to our observation, they are likely to fall off rather than be rudimentary.

At first glance, it is easy to confuse *Ulota angusti-limbata* with *U. rubella* which is endemic to the same region, but in the latter, the leaves (2.7–2.9 mm) and the capsules (1.8–2.5 mm) are both distinctly longer, capsules strongly constricted when dry and calyptra sparsely hairy. All *Ulota* species in Papua New Guinea have very

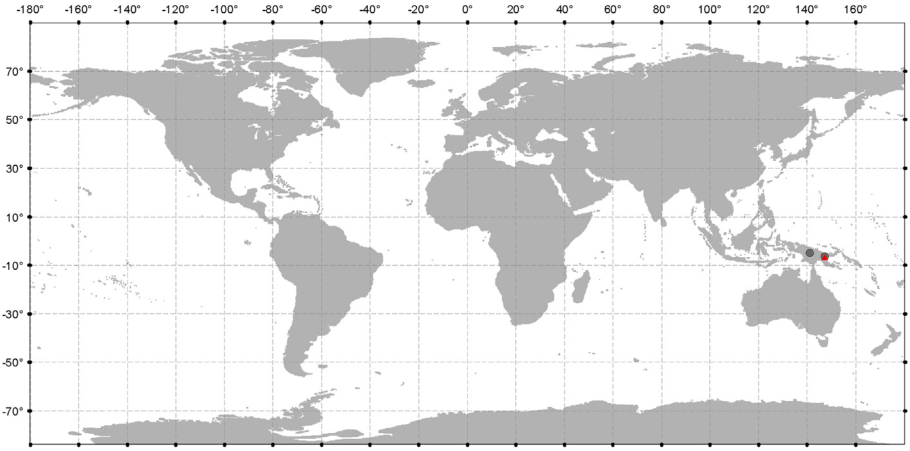


Fig. 26 – Distribution of *Ulota angusti-limbata* worldwide. The red triangle indicates the type locality.

long seta (6–10.5 mm), which is rare in the genus, except *U. novo-guinensis* (ca. 4 mm). Outside Papua New Guinea, *Ulota obtusiuscula* from North America has the longest seta, up to 9 mm. However, it differs in the larger plants (1–3.5 cm), with more rows of hyaline cells at the leaf base (3–7 rows) and smaller spores (27–30 μm). In addition, *Ulota angusti-limbata* is also similar to *U. yunnanensis*, which is endemic to China. They both have strongly crisped leaves, rounded leaf bases, a few rows of hyaline leaf basal marginal cells, short-cylindrical capsules, and eight narrow endostome segments. But the difference of *Ulota yunnanensis* lies in the multicellular spores (50–65 μm), slightly scabrous or finely papillose endostome segments and naked to sparsely hairy calyptra.

No noteworthy variation within *Ulota angusti-limbata* was seen.

Key to *Ulota angusti-limbata* and its closely related species.

1. Spores multicellular, large, 46–71 μm; seta shorter, 4–5 mm........ *U. yunnanensis*
1. Spores unicellular, small, 27–42 μm; seta longer, 5–10 mm................................2
2. Leaf basal marginal cells differentiated well, often 3–7 rows; capsules with long neck; endostome segments slightly scabrous inside; spores smaller, 27–30 μm; plants large, 1–3.5 cm.. *U. obtusiuscula*
2. Leaf basal marginal cells differentiated weakly, only 1–3 rows; capsules with short neck; endostome segments smooth inside; spores large, 35–42 μm; plants small, 0.5–2 cm..3
3. Capsules cylindrical, strongly constricted when dry; leaves longer, 2.7–2.9 mm; calyptra sparsely hairy.. *U. rubella*
3. Capsules short-cylindrical, more or less constricted when dry; leaves shorter, 2.2–2.4 mm; calyptra densely hairy.................................. *U. angusti-limbata*

Additional Specimens Examined: **Papua New Guinea**. Morobe: Mt. Sarawaket, 147°07′ E, 6°21′ S, Jul. 1981, *D. H. Norris 62727D* (H), 5 Jul. 1981, *62578* (H), *62579* (H), *62580* (H), *62581* (H), 6 Jul. 1981, *62727B* (H), *62727c* (H), 9 Jul. 1981, *63315* (H), *63320* (H), *63321* (H). Sandaun: West Sepik Distr., Star Mts., 14 Apr. 1975, *A. Touw 16239* (H), 15 Apr. 1975, *16274* (H, S).

2. **Ulota barclayi** Mitt., J. Linn. Soc., Bot. 8: 26–27. 1864. Type: U.S.A., Alaska, Sitka, *Barclay s.n.* (holotype, NY; isotypes, BM000982364–66! FH!).

Plants ca. 1 cm tall, light-brown above, and brown to black below. Stems usually branched. Leaves erect-appressed to flexuose when dry, erect-spreading to patent when moist, (1.4–) 1.6–1.8 (–2.1) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex acute; leaf plane, rarely partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, (6–) 9–12 (–17) × (5–) 7–10 (–15) μm, thick-walled, often with low simple papillae; basal inner cells linear, rectangular to elongate- rectangular, (12–) 28–46 (–73) × 2–6 (–9) μm, with moderately thickened wall, smooth; basal marginal cells differentiated in (2–) 6–9 (–12) rows hyaline, quadrate to rectangular, with thin walls.

Autoicous. Perichaetial leaves much longer, (2–) 2.2–2.4 (–2.5) mm. Vaginula not seen. Seta (1.5–) 2–3.3 (–3.5) mm long, slightly twisted anticlockwise when dry. Capsule fully emergent to short exserted, 1.2–2 (–2.2) mm long. Urn cylindrical, strongly constricted below the mouth when dry and empty, with eight furrows along the entire length, with prominent ribs alternately. Neck slightly long, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, four to five cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the transition zone between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, often recurved and lying on the exothecium when dry, lanceolate, densely and evenly papillose on both sides. Endostome segments 8, linear-lanceolate, 2/3 to almost reaching the exostome teeth, uniseriate upper, irregularly biseriate at the base, hyaline, variably incurved when dry, smooth on the outside surface, slightly scabrous on the inside surface. Opercula with a short beak. Calyptra mitrate, sparsely hairy near the apex, rarely naked. Spores spherical, finely papillose, (16–) 19–25 (–27) μm in diameter.

Illustration: Vitt (1970); figures 27 and 28.

Habitat: It grows on trunks, branches, or twigs of trees and shrubs, such as *Acer*, *Alnus* (alder), pines, and spruce. There are a few records of altitude: 10–396 m. It may occur mixed with *Ulota crispa*, *U. drummondii*, and *U. megalospora*.

Distribution: It occurs on the west coast of North America with rarely extends to the central region. Figure 29.

Notes: The species status of *Ulota barclayi* has been questioned (Anderson *et al.*, 1990; Vitt, 1970; Sullivant, 1874) for a long time until recently (Vitt, 2003, 2014), because it is easily confused with *U. japonica* from East Asia in morphology. They indeed share some characteristics, including small plants (up to 1 cm), non-crisped leaves, 6–10 rows of hyaline cells in leaf base, strongly constricted capsules, eight

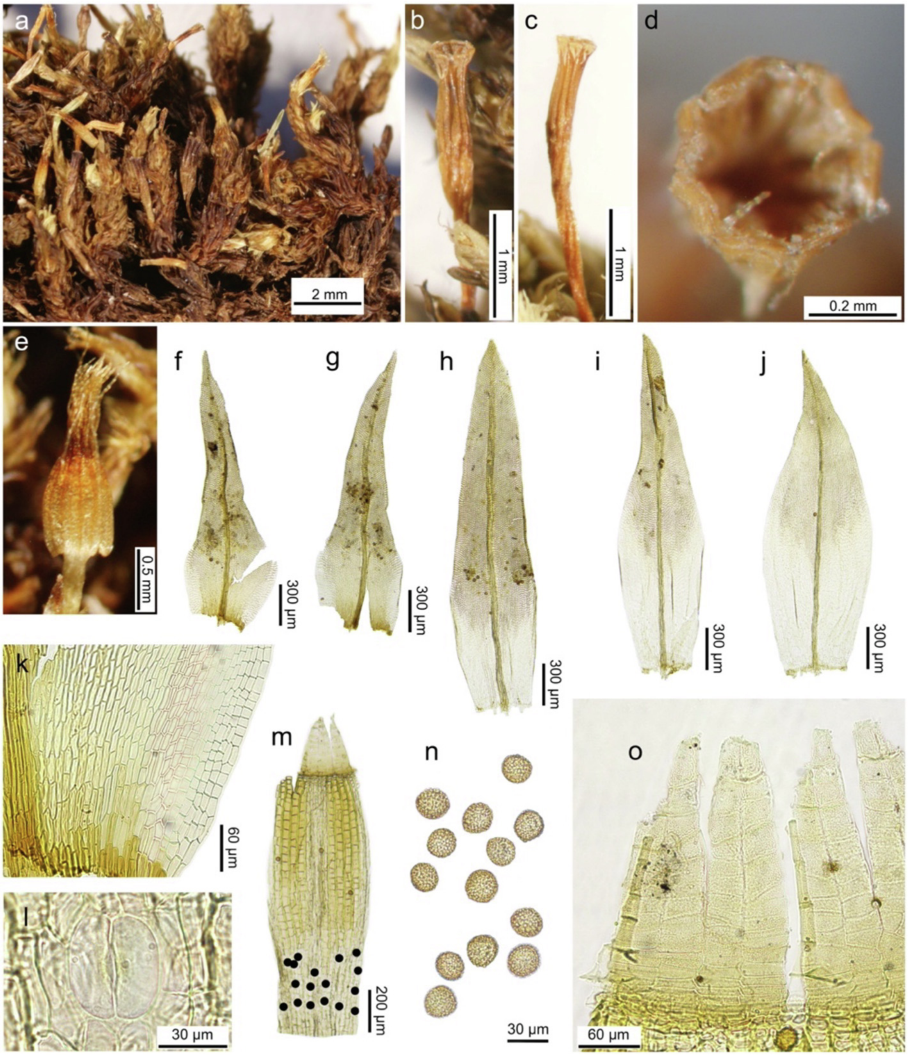


Fig. 27 – *Ulota barclayi* Mitt. a. Habit. b–c. Capsules in dry and empty. d. Capsule mouth viewed from above, with most endostome segments fallen. e. Calyptra. f–g. Leaves. h. Outer perichaetial leaves. i–j. Inner perichaetial leaves. k. Leaf basal cells. l. Stoma. m. Exothecial wall, with dots indicating stoma position. n. Spores. o. Peristome. (All from the isotype in FH except a–c and e from *W. B. Schofield 86158* [non-type, DUKE]).

narrow endostome segments, sparsely hairy calyptra, and small spores (19–25) μm. However, *Ulota japonica* is different from *U. barclayi* in the more flexuose (never appressed-erect) leaves, acuminate leaf apex, hyaline leaf basal cells with distinctly thickened transverse walls and hardly differentiated perichaetial leaves. *Ulota barclayi* also resembles *U. macrocalycina* from South America in the more appressed-erect leaves, hyaline leaf basal cells with thin walls, distinctly

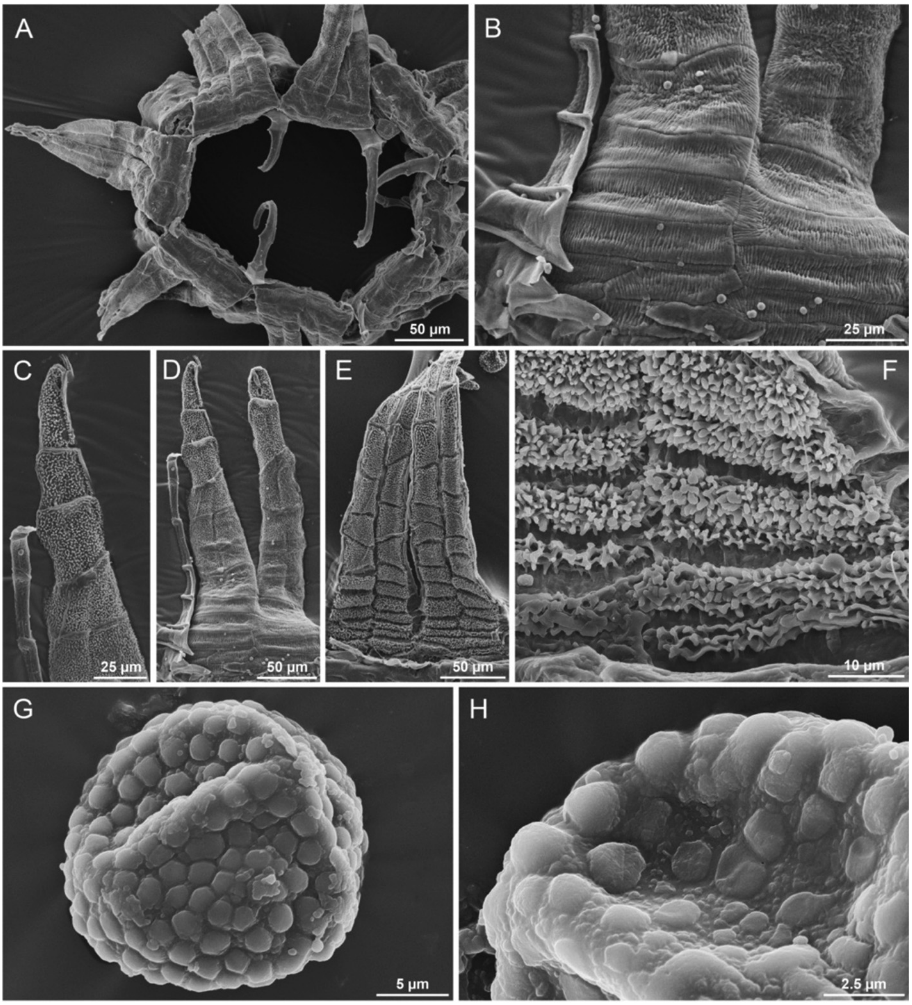


FIG. 28 – *Ulota barclayi* Mitt. A, capsule mouth; B, inner surface of basal peristome; C, inner surface of upper peristome; D, inner surface of whole peristome; E, outer surface of exostome; F, outer surface of basal exostome; G, a spore; H, surface ornamentation of a spore. (All from *W. B. Schofield 86158* [non-type, DUKE]).

differentiated perichaetial leaves, strongly constricted capsules, and eight narrow endostome segments. But the latter is distinguished in the stomata scattered on the urn, always naked calyptra and large spores (29–33 μm).

Ulota barclayi has only been known from the west coast before (Vitt, 2003, 2014), but we found two specimens from central and eastern North America, and their morphology is basically consistent with that of the west coast.

No noteworthy variation within *Ulota barclayi* was seen.

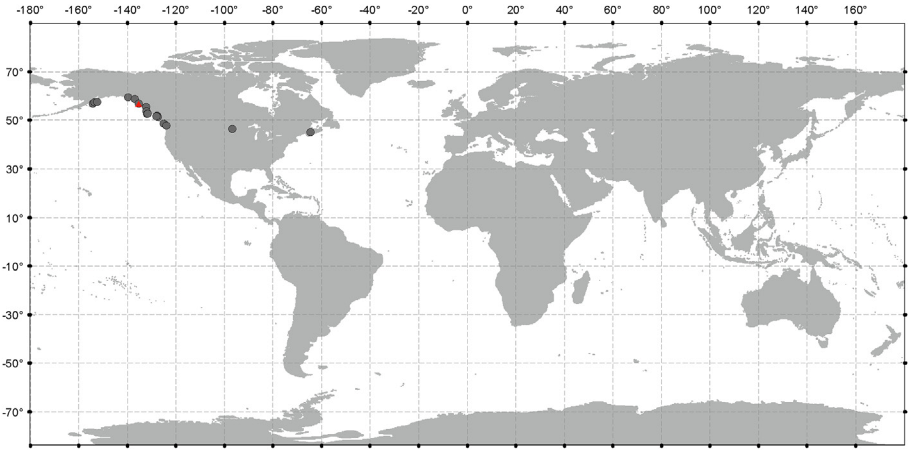


FIG. 29 – Distribution of *Ulota barclayi* worldwide. The red triangle indicates the type locality.

Key to *Ulota barclayi* and its closely related species.

1. Stomata scattered on the urn; calyptra always naked; spores relatively large, 29–33 µm... *U. macrocalycina*
1. Stomata restricted on the transition zone between urn and neck; calyptra often sparsely hairy, sometimes or rarely naked; spores small, 19–25 µm.....................2
2. Leaves flexuose, sometimes crisped when dry; leaf basal marginal cells with only thickened transverse walls; perichaetial leaves hardly differentiated........... .... *U. japonica*
2. Leaves appressed-erect to flexuose when dry; leaf basal marginal cells with thin walls; perichaetial leaves distinctly differentiated.............................. *U. barclayi*

Additional Specimens Examined: **Canada**. BRITISH COLUMBIA: Central Coast, Dawson's Landing, 51°35′ N, 127°40′ W, 2 Aug. 1986, *W. B. Schofield 85988-3* (UBC), Namu Lake, 51°51′ N, 127°51′ W, 4 Aug. 1986, *W. B. Schofield 86158-2* (UBC). NOVA SCOTIA: Kings Co., Cambridge Station, 64°38′ W, 45°04′ N, 28 Jun. 1986, *W. B. Schofield 84920-2* (UBC).

U.S.A. ALASKA: Glacier Bay National Monument, 17–18 Jul. 1969, *I. A. Worley & G. Streueler 13035-2* (UBC); Kodiak Island, U. S. Naval Reservation, 8 Jun. 1968, *A. J. Sharp 38* (UBC); Yakutat, 2 Apr. 1946, *Harriet Stair-Mazaika 5118* (MICH). WASHINGTON: Olympic National Park, Hoh Valley, 26 Oct. 1954, *G. W. Sharpe s.n.* (MICH).

3. **ULOTA BILLBUCKII** Garilleti, Mazimpaka & F. Lara, Bryologist 115(4): 587. 2012. TYPE: CHILE. Región de Magallanes y de La Antártica Chilena. Provincia Antártica Chilena, Comuna de Cabo de Hornos. Parque Nacional Alberto de Agostini, north-central west of Isla Hoste, ca. 5 km W of the eastern tip of Isla

Gordon along SW arm of Beagle Channel in unnamed sound, 55°00′22″ S, 69°12′11″ W, 2 m a.s.l., branches of *Nothofagus antarctica*, 19 Jan. 2012, *R. Garilleti s.n.* (holotype, NY; isotype, VAL).

Plants less than 2 cm tall, green above, brown below. Stems usually branched. Leaves erect to flexuose when dry, erect-patent to patent when moist, 0.8–2.1 mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded to oblong, (6–) 9–13 (–14) × (7–) 9–12 (–13) μm, thick-walled, often with low simple papillae; basal inner cells linear or rectangular, (14–) 18–27 (–33) × (3–) 5–7 (–10) μm, with thick wall, smooth; basal marginal cells weakly differentiated, often one row, hyaline, quadrate to rectangular, with longitudinal and transverse walls equally thickened.

Autoicous. Perichaetial leaves are somewhat longer, 2.1–2.5 mm. Vaginula not seen. Seta ca. 2 mm long, twisted anticlockwise when dry. Capsule long exserted, ca. 1.3 mm long. Urn cylindrical, strongly constricted below the mouth when dry and empty, eight furrows along the entire length, with prominent ribs alternately. Neck short, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as urn, about four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the urn. Preperistome not seen. Peristome double. Exostome teeth 16, united into 8 pairs, recurved when dry, often lying on the exothecium, lanceolate, densely and finely papillose on the outside, striate on the inside. Endostome segments 16, lanceolate, united by some irregularly shaped cells at the lower half part, eight segments often irregularly biseriate, as wide as teeth, eight alternately uniseriate, little narrower than teeth, hyaline, variably incurved when dry, smooth outside, finely striate inside. Opercula with a short beak. Calyptra mitrate, moderately to densely hairy. Spores irregularly globose, slightly papillose, very large, (69–) 85–99 (–113) μm in diameter, multicellular.

Illustration: Garilleti *et al.* (2012); figure 30.

Habitat: It grows on trunks or branches of trees, such as *Nothofagus*. There are only two records of altitude in this study: 2–1021 m.

Distribution: It is only known in Argentina and Chile. Figure 31.

Notes: *Ulota billbuckii* was originally described based on the large multicellular spores and the 16 broad endostome segments united by some cells at the lower part (Garilleti *et al.*, 2012). Wang and Jia (2016) cited three additional specimens of this species, but only one was confirmed here, and its stomata were located at the urn.

Ulota billbuckii is similar to *U. magellanica*, including the non-crisped leaves, few rows of hyaline cells at the basal leaf margin, 16 broad endostome segments, and large spores. However, *Ulota magellanica* differs in the free endostome segments, longer seta (2.5–3.4 mm), and unicellular spores (36–44 μm). Shorter capsules (1.0–1.2 mm), shorter vaginula hairs, and shorter axillary hairs in *Ulota billbuckii* mentioned by Garilleti *et al.* (2015) have not been seen by us so far.

Actually, *Ulota billbuckii* is very similar to *U. larrainii*, which was described recently (Garilleti *et al.*, 2015) based on apparently only the type specimens. In addition to the similarities with *Ulota magellanica* mentioned above, *U. billbuckii* and *U. larrainii* also share multicellular spores. Garilleti *et al.* (2015) suggested that

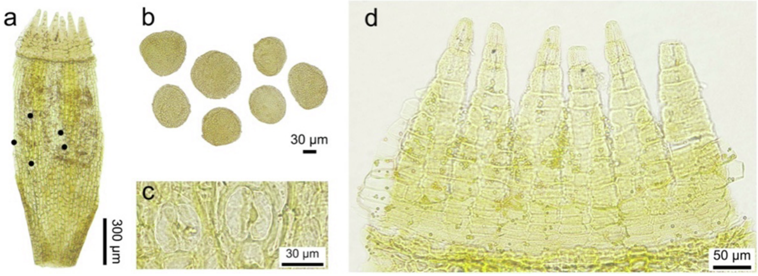


Fig. 30 – *Ulota billbuckii* Garilleti, Mazimpaka & F. Lara. a. Exothecial wall, with dots indicating stoma position. b. Spores. c. Stomata. d. Peristome. (All from *C. J. Cox no.595/00 (2)* [non-type, DUKE]).

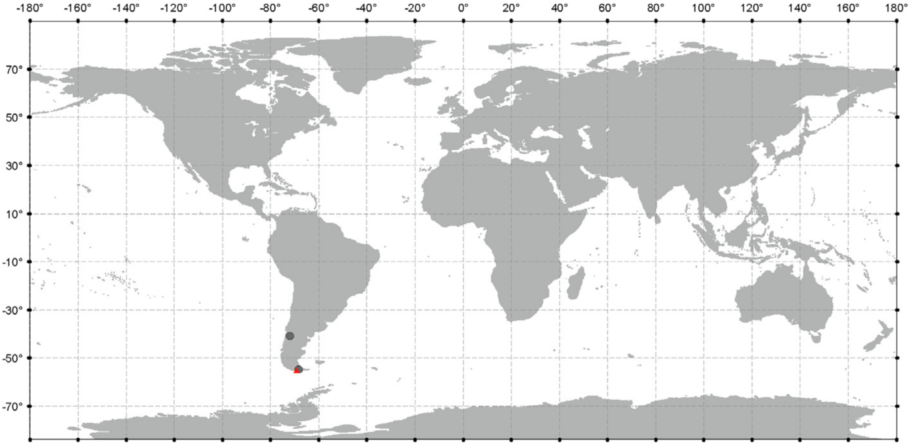


Fig. 31 – Distribution of *Ulota billbuckii* worldwide. The red triangle indicates the type locality.

in *Ulota billbuckii* the eight paired exostome teeth completely split into 16 when dry, endostome segments have a remarkably tall continuous basal ring, and spores are oblong or irregularly elongate, while in *U. larrainii* exostome teeth keep in pairs when dry, endostome segments are free at the base and spores are mostly rounded in shape. Unfortunately, we have not seen any specimen of *Ulota larrainii* so far, and its characters used in the key below is based on the detailed description in Garilleti *et al.* (2015).

Key to *Ulota billbuckii* and its closely related species.

1. Spores unicellular, 36–44 µm...*U. magellanica*

1. Spores multicellular, 85–140 µm...2

2. Endostome segments almost free at the base..................................*U. larrainii*

2. Endostome segments remarkably connected by some cells at lower half part...*U. billbuckii*

Additional Specimens Examined: **Argentina**. Tierra del Fuego: Ushuaia, 23 Dec. 1999, *D. H. Norris 98079* (H).

Chile. Los Lagos: Osorno, 40°46′48″ S, 72°12′50″ W, 23 Mar. 2000, *C. J. Cox 595/00(2)* (DUKE).

4. **Ulota bruchii** Hornsch. ex Brid., Bryol. Univ. 1: 794. 1827. Type citation: "Circa Bipontium in arboribus caespitosam clar. Bruch detexit, clar. Funck etiam in monte Pinifero legit et communicavit." (not located).

Plants 1–1.5 cm tall, yellowish green above, brown to black below. Stems usually branched. Leaves strongly crisped when dry, patent when moist, (2.3–) 2.7–3.4 (–3.7) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex long acuminate; leaf margin plane or slightly partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells round to oblong, (6–) 10–14 (–17) × (6–) 7–10 (–13) μm, thick-walled, often with two low simple papillae per cell; basal inner cells linear, rectangular to vermicular, (18–) 26–32 (–42) × (3–) 5–6 (–7) μm, with strongly thickened wall, smooth; basal marginal cells differentiated in (2) 4–7 (11) rows hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves somewhat longer, (3.1–) 3.3–3.8 (–4.1) mm. Vaginula is more or less hairy. Seta (2.5–) 3.5–4.7 (–6) mm long, twisted anticlockwise when dry. Capsule long exserted, (2.1–) 2.3–2.8 mm long. Urn cylindrical, often little puckered at the mouth, slightly to strongly constricted below the mouth when dry and empty, eight furrows along the entire length, with prominent ribs alternately. Neck long when the capsule is empty, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the transition zone between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved and laid on the exothecium when dry, lanceolate, densely papillose to papillose-reticulate near apex on the outside, papillose above and striate below on the inside. Endostome segments 8, linear to linear-lanceolate, as tall as the exostome teeth, uniseriate, often 1/4 width of teeth in the middle, hyaline, variably incurved when dry, smooth on the outside surface, scabrous above and striate below on the inside surface. Opercula with a short or medium-long beak. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (17–) 21–24 (–28) μm in diameter.

Illustration: Nyholm (1960); figures 32 and 33.

Habitat: It often grows on branches or trunks of trees, such as birch, elm, *Fraxinus* (ash), hazel, *Quercus* and *Salix*. There are few records of altitude, ranging from 120 to 590 m. It sometimes occurs with *Ulota crispa* together.

Distribution: It is only common in Europe, including Denmark, Germany, Ireland, Maderia (Portugal), Sweden, and U.K. Figure 34.

Notes: *Ulota bruchii* is a currently widely recognized species in Europe, although there have been some controversies before (Garilleti *et al.*, 2000; Smith and Proctor, 1993; Rosman-Hartog and Touw, 1987; Smith and Hill, 1975).

The most important characteristics of *Ulota bruchii* is that the capsule has a long neck when it is dry and empty, as well as a slightly narrowed mouth and the longitudinal striolate at the basal inner surface of endostome segments (Fedosov and Ignatova, 2018; Garilleti *et al.*, 2000) although the last character sometimes has not been seen clearly under light microscope.

Ulota bruchii is very similar to *U. crispa*, even though there is somewhat overlap between them, which makes some plants cannot be confidently ascribed to one or other of these two species. For example, the capsule in *Ulota bruchii* often has a long neck, while those in *U. crispa* have a short neck. However, this is not strictly consistent in *Ulota bruchii*, according to our study. In some specimens, the neck is not distinctly long, but their other characters agree well with *Ulota bruchii*. Additionally, the endostome segments of *Ulota crispa* in some cases, also have longitudinal striolate at the base. In conclusion, we considered that the relationship between *Ulota bruchii* and *U. crispa* is worth further study.

The long capsule neck of *Ulota bruchii* seems to be caused by the hollow of the capsule seta in the upper part (figure 32a–c), which is similar to *U. eurystoma* and *U. yakushimensis* from Japan. However, *Ulota eurystoma* differs in the funnel-shaped capsules with wide-mouth which never constricted when dry and empty, while *U. yakushimensis* differs in the subglobose capsules, absence of endostome segments and large multicellular spores (79–91 μm). Moreover, its long capsule neck in *Ulota bruchii* also resembles *U. drummondii*, but the latter is distinguished by the non-crisped leaves and the rudimentary or absent endostome segments.

The neck length of *Ulota bruchii* varies to some extent, see above.

Key to *Ulota bruchii* and its closely related species.

1. Leaves erect to flexuose when dry; endostome segments rudimentary or absent........2
1. Leaves strongly crisped when dry; endostome segments well-developed..........3
2. Capsules long cylindrical, puckered mouth, distinctly constricted when dry; spores small, 24–27 μm, unicellular........*U. drummondii*
2. Capsules subglobose, wide mouth, hardly constricted below the mouth when dry; spores large, 79–91 μm, multicellular........*U. yakushimensis*
3. Capsules obovoid to subglobose, not constricted when dry; exostome teeth wrinkle outside and striolate inside........*U. eurystoma*
3. Capsules cylindrical, moderately to strongly constricted when dry; exostome teeth densely papillose outside and papillose to striate inside........ 4
4. Capsules with short neck when dry and empty; endostome segments often scabrous to nearly smooth at the base........*U. crispa*
4. Capsules with long neck when dry and empty; endostome segments often with longitudinally striolate at the base........*U. bruchii*

Additional Specimens Examined: **Denmark**. ZEALAND REGION: Storskoven ved Hvalsø, Jan. 1881, *C. Jensen s.n.* (UBC), 27 Oct. 1901, *C. Jensen s.n.* (UBC).

Germany. BADEN-WÜRTTEMBERG: in sylv. Hercyniae, *s.coll.* (H). BAVARIA: Hinterstein, 22 Sep. 1972, *A. V. Hübschmann s.n.* (UBC). RHEINLAND-PFALZ: *s.d.*, *s.coll.* (JE). THÜRINGEN: Jena, Jul. 1902, *W. Trantinann s.n.-1* (S).

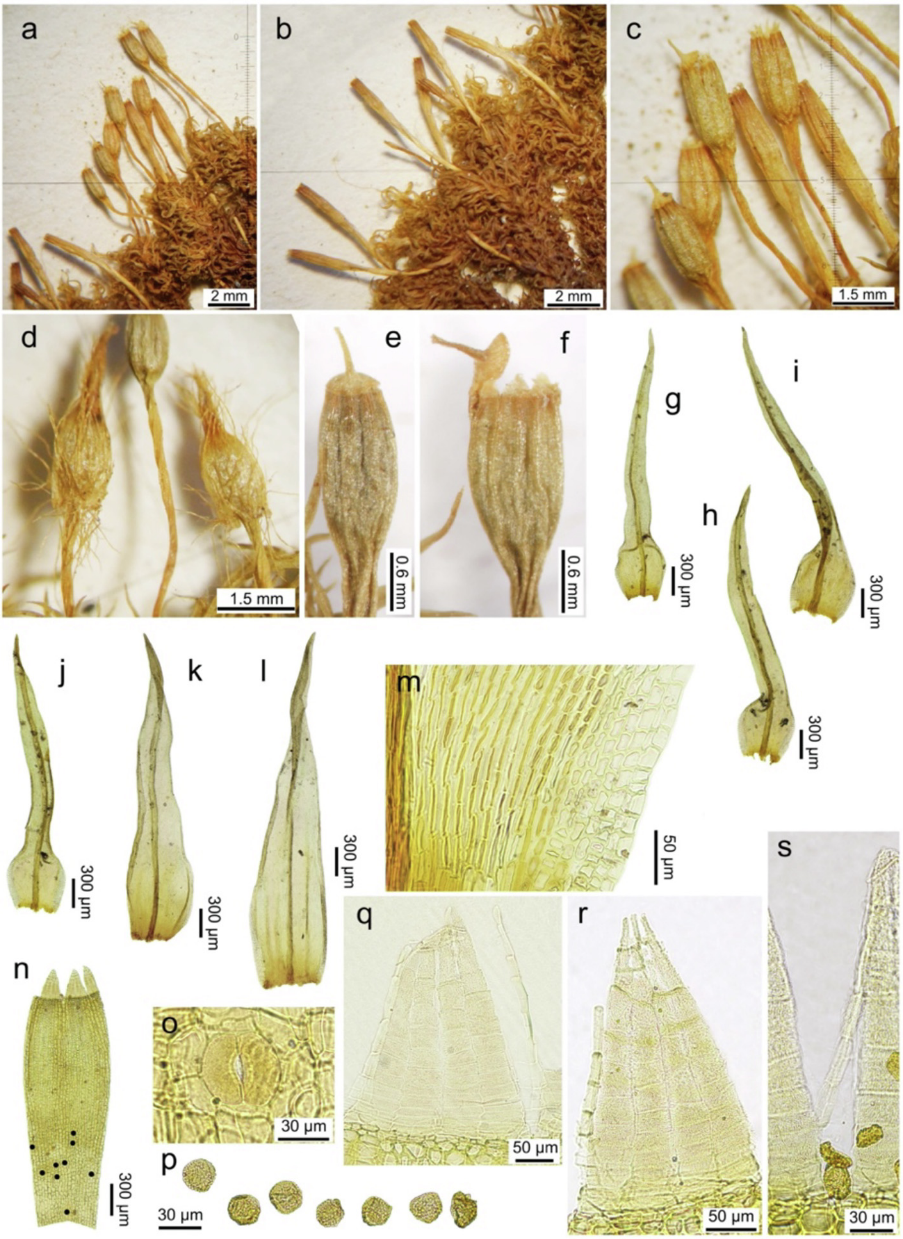


FIG. 32 – *Ulota bruchii* Hornsch. ex Brid. a–b. Habit. c. Capsules in dry. d. Calyptra. e–f. Capsules with opercula. g–j. Leaves. k–l. Perichaetial leaves. m. Marginal cells at leaf base. n. Exothecial wall, with dots indicating stomata position. o. Stoma. p. Spores. q–r. Peristomes. s. Endostome segment with striate at the base. (a–d from *s.coll.* [non-type, FI], e, f and m from *s.coll.* [non-type, JE], h, j, n, r and o from *W. Smith s.n.* [non-type, NSW], g, i and q from *s.coll.* [non-type, HBG], k, l, p and s from *W. B. Waterfall 322* [non-type, NSW]).

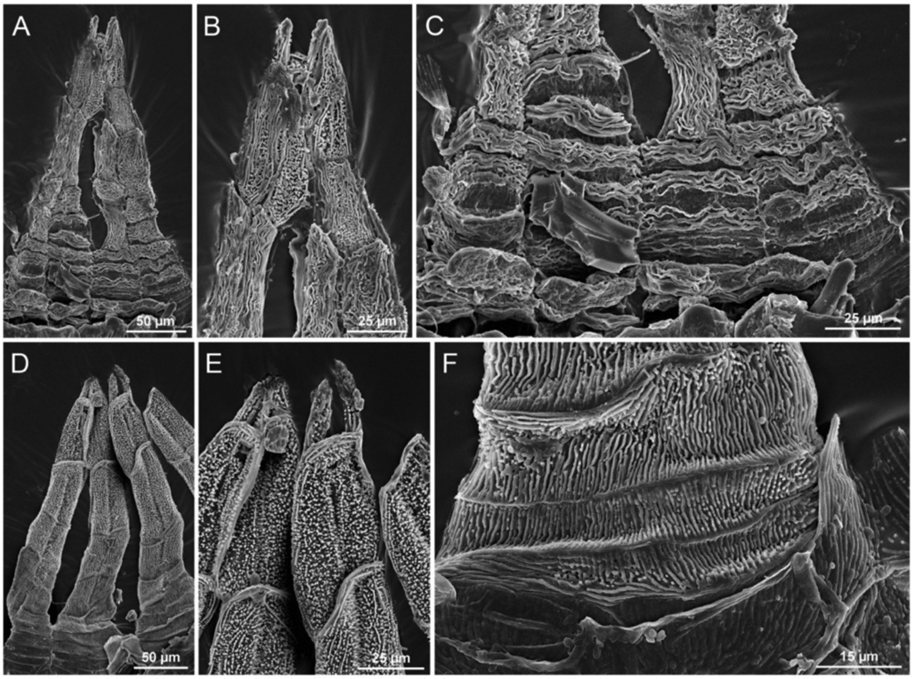


FIG. 33 – *Ulota bruchii* Hornsch. ex Brid. A, outer surface of exostome; B, outer surface of upper exostome; C, outer surface of basal exostome; D, inner surface of exostome; E, inner surface of upper exostome; F, inner surface of basal exostome and endostome. (All from *R. Lehr* [non-type, HBG]).

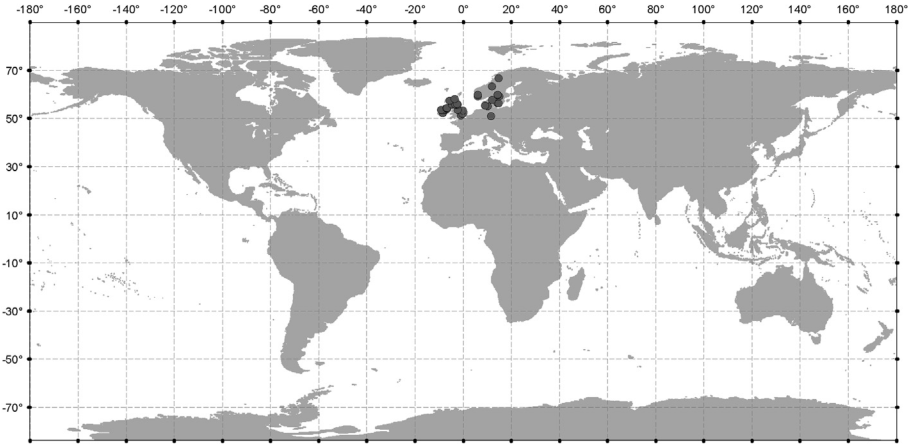


FIG. 34 – Distribution of *Ulota bruchii* worldwide.

Ireland. Connacht: Lough Mask, 21 May 2003, *D. T. Holyoak s.n.* (BBSUK). Leinster: Westmeath Co., 26 Aug. 2007, *D. T. Holyoak 07-130* (BBSUK); Lough Ree, St. John's Wood, 5 Jul. 2002, *N. G. Hodgetts s.n.* (BBSUK). Ulster: Monaghan Co., Annaghmakerrig Forest, 5 Aug. 2005, *S. D. S. Bosanquet, C. D. Preston, R. D. Porley, S. J. Thomas & R. S. Weyl s.n.* (BBSUK), W. side of Lough Egish, 5 Aug. 2005, *S. D. S. Bosanquet, C. D. Preston, R. D. Porley, S. J. Thomas & R. S. Weyl s.n.* (BBSUK).

Norway. Hordaland: Kvinnherad, Rosendal, Melsdalen, 20 Jul. 2004, *L. Hedenäs s.n.* (S); Krossdal, 11 Jul. 1947, *Sten Ahlner s.n.* (S). Nordland: Rana herad, 25 Jul. 1971, *R. Alava 10108* (UBC).

Sweden. Blekinge: Ringamåla, 6 Aug. 1917, *S. Medelius s.n.* (UBC). Jämtland: Åre, 63°20′ N, 12°04′ E, 27 Jul. 2006, *L. Hedenäs & I. Bisang s.n.* (S). Närke: Hidinge, 6 Sep. 2007, *T. Hallingbäck 45182* (S). Skåne: Hjärsås, 23 Jun. 1946, *R. Alava s.n.* (UBC). Värmland: Filipstad, 59°51.806′ N, 14°16.884′ E, 31 Aug. 2010, *L. Hedenäs & G. Odelvik s.n.* (S), 59°36.332′ N, 14°13.518′ E, 1 Sep. 2010, *L. Hedenäs & G. Odelvik s.n.* (S). Västergötland: Göteborg, Nov. 1913, *E. Hjertman s.n.* (H).

U.K. England: College Wood, 16 Feb. 2001, *F. A. Higgs s.n.* (BBSUK). Scotland: East Lothian, 13 May 1911, *W. Evans s.n.* (E), Nov. 1967, *U. K. Duncan s.n.* (E), 8 Jan. 1995, *D. G. Long 25830* (E); Midlothian, 13 Jan. 1974, *D. G. Long 3060* (E), 20 Sep. 2003, *D. F. Chamberlain s.n.* (E); Selkirkshire, 10 Apr. 1997, *D. G. Long 26738* (E); Stirlingshine, Wharry Glen, 12 Feb. 1898, *W. Evans s.n.* (E), 7 Feb. 1953, *A. C. Cucendwell s.n.* (E); Sutherland, Torridon, 11 Sep. 1944, *W. Ross s.n.* (E).

5. **Ulota calvescens** Wilson, Bryoth. Eur. 11: 520. 1862. Type: Ireland. Tore mountain, May 1861, *Dr. Carrington* (holotype, BM000982355! isotypes, M0138782! HBG!).

Ulota paivana Schimp., Flora 69: 347. 1886. *invalid, cited as synonym.* ***syn. nov.*** Type: Portugal. Madeira, Boroaca, 16 Jan. 1866, *A. Paiva s.n.* (holotype, BM000982376!)

Weissia vittata (Mitt.) Lindb., J. Bot. 11: 200, 202. 1873. ≡ *Orthotrichum vittatum* (Mitt.) Mitt., Nat. Hist.Azores 299. 1870. ≡ *Ulota vittata* Mitt., J. Proc. Linn. Soc., Bot. 8: 3. 1864. Type: Portugal. Madeira, on trees on the mountains, *J. Y. Johnson* (holotype, NY).

Plants 0.5–1.5 cm tall, green above, brown to black below. Stems usually branched. Leaves strongly crisped when dry, erect-spreading to patent when moist, (2.4–) 2.9–3.3 (–3.7) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex long acuminate; leaf margin plane or slightly partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells round to oblong, (6–) 8–11 (–14) × (6–) 7–8 (–10) μm, thick-walled, smooth, rarely with low simple papillose; often 3–4 rows elongate cells inside the margin, ascending above the base, usually up to central part of leaf; basal inner cells linear, rectangular to elongate-rectangular, (19–) 26–35 (–49) × (4–) 5–7 (–9) μm, with moderately thickened wall, smooth; basal marginal cells differentiated in (1) 3–6 (10) rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves are slightly longer, (2.8–) 2.9–3.8 (–3.9) mm. Vaginula naked. Seta (3.5–) 4–5.5 mm long, twisted anticlockwise when dry. Capsule long exserted. Urn cylindrical, ca. 1.5 mm long, yellow to brown, often strongly constricted below the mouth when dry and empty, eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the transition zone between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved and lying on the exothecium when dry, lanceolate, densely papillose to papillose-reticulate near apex on the outside, finely papillose or sometimes papillose-striate above and prominently vertically-striate below on the inside. Endostome segments 8, linear, as tall as the exostome teeth, uniseriate, often 1/4 width of teeth in the middle, hyaline, variably incurved when dry, smooth on the outside surface, slightly scabrous on the inside surface. Opercula with a short or medium-long beak. Calyptra mitrate, often sparsely hairy. Spores spherical, finely papillose, (14–) 17–22 (–24) μm in diameter.

Illustration: Smith (1978); figures 35 and 36.

Habitat: It grows on branches, twigs, or trunks of trees, such as elm, hazel, *Laurus*, *Persea*, *Rhamnus*, *Spartium*, and *Salix* (willow). There are some records of altitude: (7–) 155–1300 (–2000) m. It is occasionally mixed with *Orthotrichum lyellii.*

Distribution: It is **endemic** along the Atlantic coast of Europe, including Maderia (Portugal), Ireland, and U.K. Figure 37.

Notes: *Ulota calvescens* can be identified by its obviously differentiated marginal hyaline cells at the leaf base, strongly striate exostome teeth, and sparsely hairy calyptra. Additionally, *Ulota calvescens* has a band of elongated cells that ascends the margin of the leaves above the basal part, reaching to mid-leaf (figure 35l). This is a reliable diagnostic character confirmed by Blockeel and Turner (2013) and us. Importantly, based on this unique character in *Ulota* and the support of molecular evidence, *Ulota calvescens* have recently been segregated as a new genus, *Atlantichella* F. Lara, Garilleti & Draper (Draper *et al.*, 2021).

Ulota calvescens resembles *U. crispa* in the strongly crisped leaves, distinctly differentiated leaf-base marginal cells, long exserted capsules and eight narrow endostome segments. *Ulota crispa* differs, however, in the more rows (5–11) of hyaline cells at the marginal leaf base, lack of elongate cells inside the leaf margin above the basal part, inconspicuously striate exostome teeth, and densely hairy calyptra.

The elongated cells inside the leaf margin above the basal part vary in length to some extent. They are occasionally very short, which makes the band indistinct. The calyptra in *Ulota calvescens* is sometimes moderately to strongly hairy. These variations were reported in detail by Holyoak (2002) and Blockeel and Turner (2013).

Key to *Ulota calvescens* and its closely related species.

1. Leaf marginal cells at the base differentiated in more rows (5–11); leaf cells above the basal part almost uniform; exostome teeth inconspicuously striate; calyptra densely hairy..*U. crispa*

1. Leaf marginal cells at the base differentiated in fewer rows (3–6); leaf cells inside the margin above the basal part becoming elongated in a few rows, forming a band ascending the margin and reaching to mid-leaf; exostome teeth prominently striate; calyptra often sparsely hairy.................................*U. calvescens*

Additional Specimens Examined: **Ireland**. Connacht: Galway Co., Slieve Aughty, 17 Jul. 1994, *N. G. Hodgetts 2961* (BBSUK); Lough Corrib, 24 May 2003, *D. T. Holyoak s.n.* (BBSUK). Leinster: Longford Co., 5 Sep. 2007, *D. T. Holyaok 07-318* (BBSUK); Offaly Co., Dunkerrin, 29 Jun. 2005, *N. G. Hodgetts 6145*

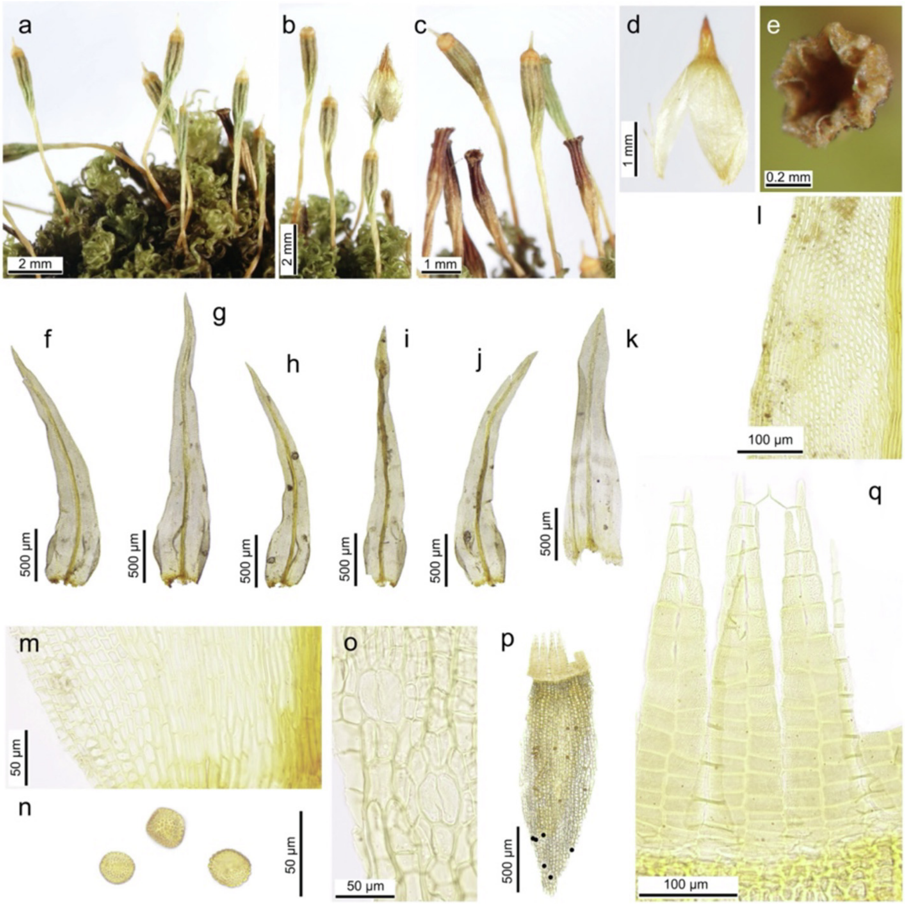


Fig. 35 – *Ulota calvescens* Wilson. a–c. Habit, with capsules in dry. d. Calyptra. e. Capsule mouth viewed from above. f–j. Leaves. k. Inner perichaetial leaf. l. Submarginal elongate cells at the middle of leaf. m. Marginal cells at leaf basa. n. Spores. o. Stomata. p. Exothecial wall, with dots indicating stoma position. q. Peristome. (a–e from *L. Hedenäs* [non-type, S], f–k from *Dr. Carrington* [non-type, HBG], l–q from *D. M.* [non-type, H]).

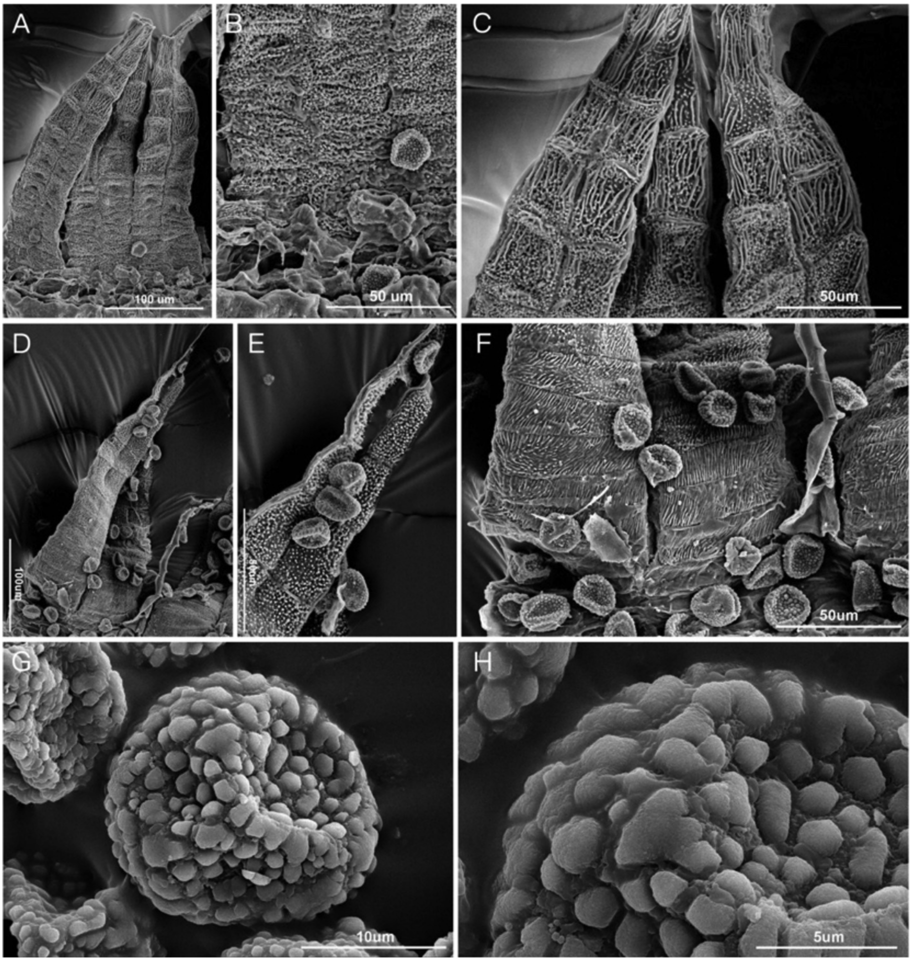


Fig. 36 – *Ulota calvescens* Wilson. A, outer surface of exostome; B, outer surface of basal exostome; C, outer surface of upper exostome; D, inner surface of endostome; E, inner surface of upper endostome; F, inner surface of basal endostome; G, spores; H, surface ornamentation of a spore. (All from the isotype in M).

(BBSUK). Munster: Attychraan River, 24 Jun. 2005, *N. G. Hodgetts 6105* (BBSUK); Clare Co., 22 Aug. 1957, *A. C. Crundwell s.n.* (PC); Kerry Co., Turk Waterfall, Jun. 1865, *s.coll.* (MICH); Killarney, 24 Jul. 1873, *S. O. Lindberg s.n.* (H), O'Sullivan's Cascade, 1885, *G. A. H. s.n.* (H), Jun. 1865, *D. M. s.n.* (H); Limerick Co., 28 Jun. 2005, *N. G. Hodgetts 6142* (BBSUK). Ulster: Monaghan Co., 28 Aug. 2007, *D. T. Holyoak 07-155* (BBSUK).

Portugal. Azorica: Salto do Cavalo, 6 Jun. 1937, *S. Miguel 98* (PC); Torrinhas, 25 Jan. 1880, *R. Fritze s.n.* (H). Maderia: Bonaventura-Pico Ruivo, 5 Jun. 1952, *H. Persson s.n.* (S); Montado do Pereiro, 17 May 1993, *L. Hedenäs* (S); Ribeira do Passo, 1 Jul. 1952, *M. Nobrega & Herman Persson s.n.* (S); São Vicente, 13 Jun. 1998, *L. Hedenäs* (S).

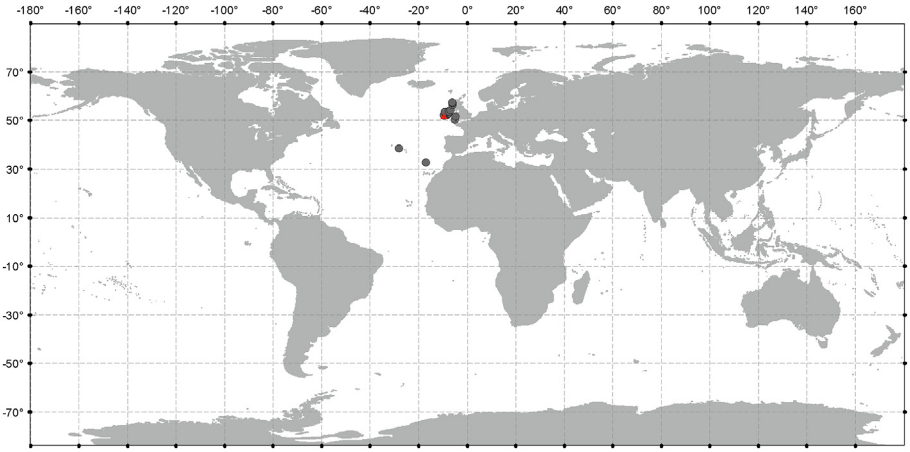


FIG. 37 – Distribution of *Ulota calvescens* worldwide. The red triangle indicates the type locality.

U.K. ENGLAND: West Cornwall, 11 Jul. 2000, *D. T. Holyoak 00-423* (BBSUK). NORTH IRELAND: Fermanagh Co., Jun. 1909, *W. N. Tetley s.n.* (PC). SCOTLAND: Beinn Mhòr, 8 Aug. 1992, *N. G. Hodgetts 2649* (BBSUK); Islands of Mull, 8 Jul. 1963, *H. Milme-Redhead s.n.* (PC); Isle of Skye, 15 Jun. 1962, *D. A. Ratcliffe s.n.* (E), 16 Jun. 1962, *s.n.-2* (E), 27 Jun. 1962, *s.n.* (E). WALES: Bosanquet, 26 Feb. 2007, *S. D. S. s.n.* (BBSUK).

6. **ULOTA COARCTATA** (P. Beauv.) Hammar, Monogr. Orthotrich. Ulot. Suec. 25. 1852. ≡ *Orthotrichum coarctatum* P. Beauv., Prodr. Aethéogam. 80. 1805. ≡ *Ulotrichum coarctatum* (P. Beauv.) Schimp., Bryol. Eur. 3: 1 (fasc. 46–47 Consp. vol. 3: I). 1851. *invalid combination.* ≡ *Weissia coarctata* (P. Beauv.) Lindb., J. Bot. 11: 200, 204. 1873. TYPE: "De l'Amérique septentrionale"comm.. *Persoon* (lectotype, G, designated by Vitt, 1970); *Richard* (paralectotype, G).

Orthotrichum clausum Hornsch., Scott. Crypt. Fl. 2: 133. 1824. invalid, cited as synonym.

Orthotrichum clavatum Bernh., Bryol. Univ. 1: 302. 1826. invalid, cited as synonym.

Orthotrichum plicatum C.F. Ludw., Bryol. Univ. 1: 302. 1826. illegitimate, later homonym.

Splachnum wulfenianum Schwägr., Sp. Musc. Frond., Suppl. 1: 46. pl. 14. 1811.

Ulota ludwigii (Brid.) Brid., Muscol. Recent. Suppl. 4: 112. 1819 [1818]. ≡ *Orthotrichum ludwigii* Brid., Muscol. Recent. Suppl. 2: 6. 1812. ≡ *Orthotrichum crispulum* var. *lugwigii* (Brid.) Hampe, Flora 20: 279. 1837. ≡ *Ulotrichum ludwigii* (Brid.) Schimp., Bryol. Eur. 3: 1 (fasc. 46–47 Consp. vol. 3: I). 1851. *invalid combination.* TYPE CITATION: "In Lufatià et circa Lipfiam ad arbores Ludwigius detexit et nobiscum communicavit"., 1811, *Ludwig* (type, B!); 1812, *Ludwig* (type, B!).

Plants 0.5–1.5 cm tall, green above, brown to black below. Stems usually branched. Leaves erect to flexuose when dry, patent when moist, (1–) 1.3–1.6 (–2.1) mm long, leaf lamina narrow lanceolate, unistratose; leaf base wide, rounded; apex long acuminate; leaf margin plane; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, (5–) 8–12 (–15) × (4–) 6–9 (–10) μm, thick-walled, smooth or with low simple papillae; basal inner cells linear, rectangular to elongate-rectangular, (13–) 20–28 (–38) × (2–) 3–4 (–5) μm, with thick wall, smooth; basal marginal cells weakly differentiated, (1–) 2–4 (–6) rows, rarely 6 rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves somewhat longer, (1.8–) 2.1–2.6 (–2.9) mm. Vaginula sparsely hairy, smooth, hyaline. Seta (3.8–) 4–4.5 mm long, twisted anticlockwise when dry. Capsule short to long exserted, 1.6–1.7 mm long. Urn pyriform, puckered, strongly constricted at the mouth when dry and empty, eight furrows only present just mouth below. Neck somewhat long, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands near the mouth, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the transition zone between urn and neck. Preperistome not seen. Peristome single. Exostome teeth 16, often united into 8 pairs, variably erect or spreading when dry, lanceolate, densely and obscurely papillose on both sides. Endostome segments are absent, rarely rudimentary, scabrous. Opercula with a beak, short to moderately long. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (18–) 22–26 (–33) μm in diameter.

Illustration: Nyholm (1960), Smith (1978), Crum and Anderson (1981) and Ireland (1982); figures 38 and 39.

Habitat: It grows on the trunk of trees, including *Acer*, *Alnus*, *Betula*, maple, *Populus*, *Salix*, and yellow birch. There are some records of altitude: (20–) 60–950 (–1524) m. It's very common to mix with *U. crispa*, sometimes with *U. drummondii* and *Orthotrichum sp.*

Distribution: It is common on both sides of the northern Atlantic and tending to spread inland, including Canada, France, Germany, Norway, Poland, Slovakia, Sweden, U.K., and U.S.A. It is also been reported in Turkey (Lara *et al.*, 2010) and European Russia (Fedosov and Ignatova, 2018) recently, but we have not seen any specimens yet. Figure 40.

Notes: *Ulota coarctata* is a unique species that is easily recognized by its pyriform capsules with the strongly puckered mouth but nearly smooth below and non-crisped leaves. These characters distinguish it from all other *Ulota* species, especially combined with the absence of endostome segments.

In *Ulota*, capsules with a puckered mouth but smooth below when dry are rare. Besides *Ulota coarctata*, *U. gymnostoma* from China and *U. rhytiore* from Central America also have this character. But these two species differ in the strongly flexuose to crisped leaves, emergent to short exserted fusiform capsules (seta 2–5 mm), and absent peristome. Moreover, stomata in *Ulota rhytiore* occur throughout the urn rather than on the transition zone between the urn and neck.

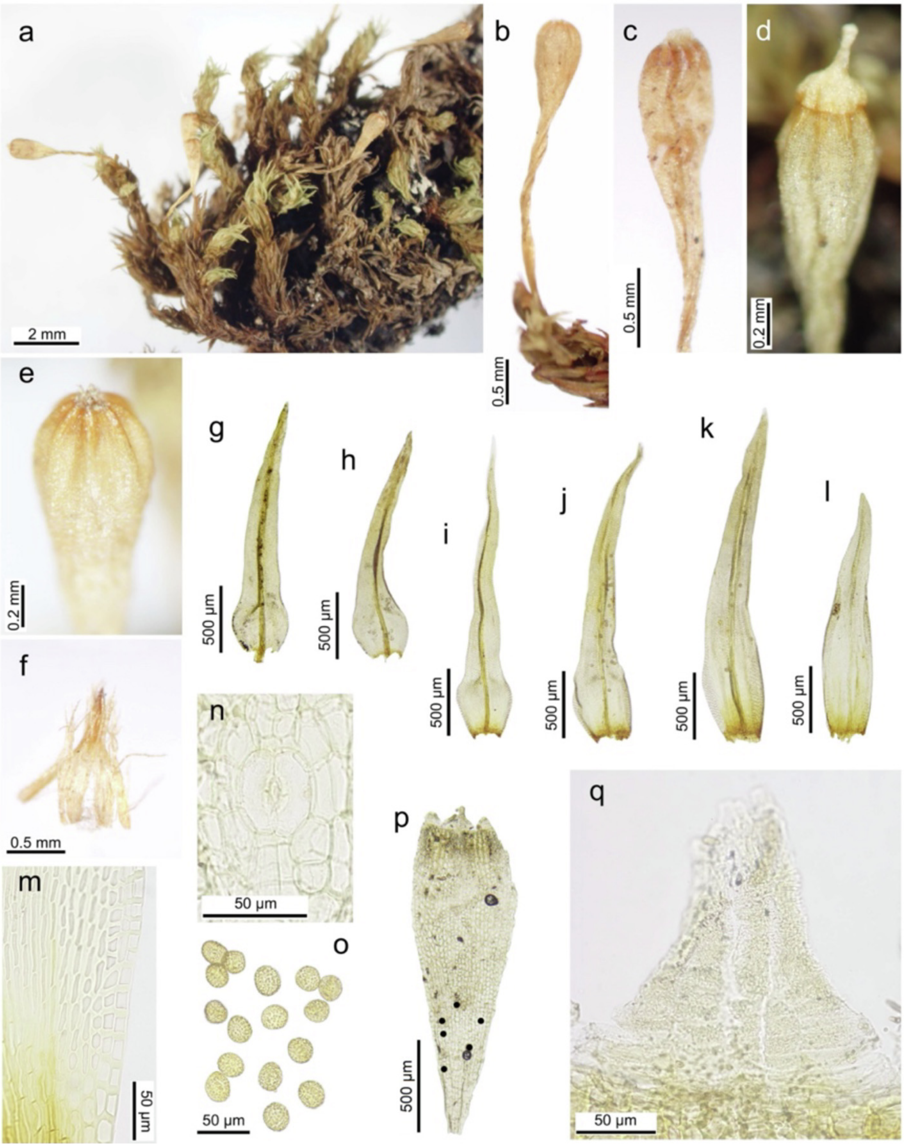


Fig. 38 – *Ulota coarctata* (P. Beauv.) Hammar. a. Habit. b. Sporophyte. c. A capsule in dry and empty. d. A capsule with an operculum. e. Puckered capsule mouth. f. Calyptra. g–j. Leaves. k. Outer perichaetial leaf. l. Inner perichaetial leaf. m. Marginal cells at leaf base. n. Stoma. o. Spores. p. Exothecial wall, with dots indicating stoma position. q. Peristome. (a–f, n, p and q from *H. Crum 9873* [non-type, PE], g–m and o from *M. Dickron* [non-type, BM]).

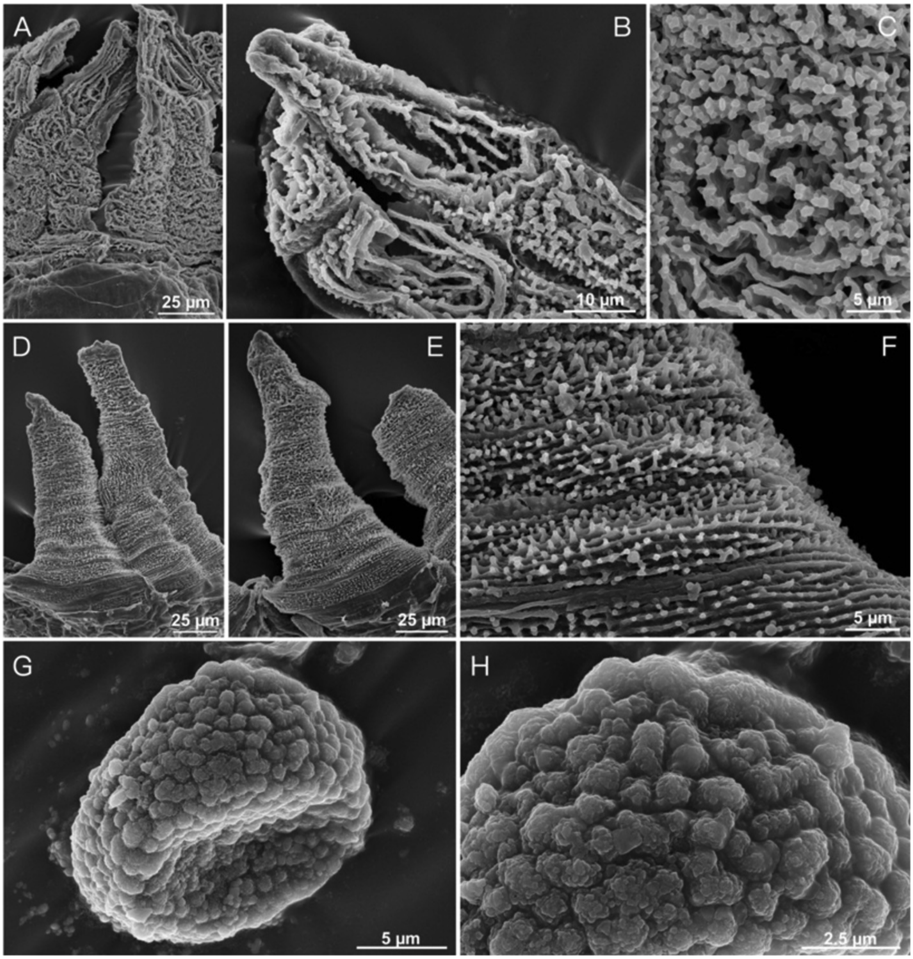


FIG. 39 – *Ulota coarctata* (P. Beauv.) Hammar. A, outer surface of exostome; B, outer surface of upper exostome; C, outer surface of basal exostome; D–E, inner surface of endostome; F, inner surface of basal endostome; G, a spore; H, surface ornamentation of a spore. (All from *J. Shaw 15435-1* [non-type, DUKE]).

Key to *Ulota coarctata* and its closely related species.

1. Capsules pyriform, short to long exserted (seta 4–4.5 mm); peristome single with exostome teeth well-developed; leaves erect to flexuose when dry.......... *U. coarctata*
1. Capsules fusiform, emergent to short exserted (seta 2–5 mm); peristome absent or sometimes rudimentary; leaves strongly flexuose to crisped when dry.......... 2

2. Leaves strongly crisped when dry; capsules fully emergent to short exserted; stomata occur on the transition zone between urn and neck........*U. gymnostoma*
2. Leaves flexuose to spiral, rarely crisped when dry; capsules emergent; stomata occur throughout the urn..*U. rhytiore*

Additional Specimens Examined: **Austria**. Tyrol: Lake Achen, 1860, *M. Huss s.n.* (H).

Canada. New Brunswick: Albert Co., Fundy National Park, 8 Jul. 1968, *R. R. Ireland 11553* (H); Carleton Co., 11 Jul. 1970, *R. R. Ireland 12879* (H, MICH); Victoria Co., 10 Jul. 1970, *R. R. Ireland 12837* (MICH); Westmorland Co., 23 Jul. 1972, *R. R. Ireland 13537* (MICH). Newfoundland: Bonavista, Port Blandford, 48°21′ N, 54°10′ W, 20 Oct. 1975, *G. R. Brassard 10522* (H, MICH); Burgeo-La Poile, Hare Bay, 21 Jun. 1949, *R. Tuomikoski 1345* (H); Fortune Bay, St. Alban's, 26 Jun. 1949, *R. Tuomikoski 1784* (H); St. Barbe's, Gros Morne National Park, 3 Jun. 1980, *R. J. Belland 2867* (UBC), 11 Sep. 1980, *3915-1* (MICH); illegible handwritten locality, 25 Aug. 1924, *B. Long 150* (MICH); St. George's-Port au Port, 5–6 Jul. 1949, *R. Tuomikoski 2484a* (H), 48°43′ N, 58°05′ W, 8–9 Jul. 1949, *2798* (H); Trinity, 2 May 1972, *J. Hancock & C. Butler 128* (MICH), Clarenville South, 20 Aug. 1956, *T. Ahti s.n.* (H), 48°06′ N, 53°57′ W, Deep Bight, 1 Jun. 2002, *W. B. Schofield 119529-2* (DUKE). Nova Scotia: Anapolis Co., 44°29′ N, 65°08′ W, 3 Aug. 1968, *R. R. Ireland 12522* (MICH); Halifax Co., Moores Lake, 6 Jul. 1929, *L. E. Wehmeyer s.n.* (MICH536849, 536857); Kings Co., 22 Jul. 1965, *W. B. Schofield* 27494-2 (UBC), 9 Aug. 1980, *W. B. Schofield & M. R. Schofield 75317* (UBC), 17 Oct. 1983, *W. B. Schofield 81637* (UBC), 45°14′ N, 64°27′ W, 18 Jul. 1987, *W. B. Schofield, R. J. Belland & S. Clayden 88239* (UBC). Ontario: Algoma Disctr., Lake Superior Provincial Park, 47°17′ N, 84°33′ W, 5 Aug. 1971, *R. R. Ireland 14917* (H, MICH, UBC), the Islands and shore of Northeastern Lake Superior, 24 Jul. 1931,

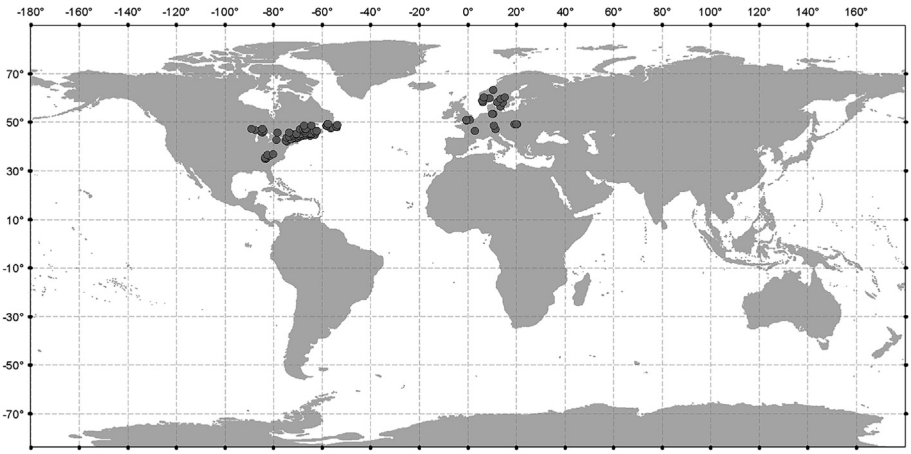


Fig. 40 – Distribution of *Ulota coarctata* worldwide.

C. O. Grassl 1380-1 (MICH); Algonquin Park, 31 Aug. 1939, *R. F. Cain 2301* (MICH). PRINCE EDWARD ISLAND: Glencorradale, 46°27′ N, 62°10′ W, 2 Aug. 1970, *R. R. Ireland 14087* (MICH); s. loc., 2 Jul. 1888, *J. Macoun s.n.-1* (MICH); Queens Co., 46°01′ N, 62°50′ W, 28 Jul. 1970, *R. R. Ireland 13829* (H), Hunter River, 46°22′ N, 63°24′ W, 25 Jul. 1970, *R. R. Ireland 13678-1* (MICH). QUEBEC: Gaspe Co., 22 Jul. 1923, *J. F. Collins 5746* (MICH); Matane Co., 16 Jul. 1923, *J. F. Collins 5698* (MICH); Terrebonne Co., 23 Aug. 1958, *H. Crum 9873* (H, MICH).

France. NOUVELLE-AQUITAINE: Eaux Bonnes, *Sprucei s.n.* (H).

Germany. HAMBURG: Heimfeld, 27 Jul. 1873, *C. T. Timm s.n.* (HBG). NORTH RHINE-WESTPHALIA: Bonn, Jan. 1869, *W. P. Alcott s.n.* (MICH).

Norway. HORDALAND: Hardanger, Jul. 1873, *R. Hartman s.n.* (H), Oct. 1873, *s.n.* (H). ROGALAND: Egersund, Jul. 1889, *N. Bryhn* (NSW). SOGN OG FJORDANE: Sogn, 10 Jul. 1867, *N. Wulfsberg s.n.* (H). TELEMARK: Vestfjorddalen, *illegible handwritten collector name 101* (H). TRØNDELAG: Trondheim (Nidaros), *J. Ångström s.n.* (H), Pref. Nidarosiensis, 1836–37, *J. Ångström s.n.* (H).

Poland. OLESNO: Kościeliska, 20 Jul. 1912, *A. Zmuda s.n.* (NSW).

Slovakia. SPIŠ: Montes Bělské Tatry, Aug. 1947, *Z. Pilous s.n.* (H). ŽILINA: Montes Malá Fatra, May 1934, *Z. Pilous s.n.* (H).

Sweden. BOHUSLÄN: Christinedal, Jul. 1863, *Thedenius s.n.* (H). DALARNA: Rämshyttan, 1844, *O. L. Jillén s.n.* (H). SMÅLAND: Ferngjo, *Aynfelt s.n.* (H). VÄRMLAND: Kyrkebol, 1852, *N. C. Kindberg s.n.* (H). VÄSTMANLAND: Viker, 18 Aug. 1966, *T. Koponen s.n.* (H).

U.K. ENGLAND: Bordon, 2 Mar. 2008, *Rvlansdaun & Fjrunsey s.n.* (BBSUK); Hamstreet, Faggs Wood, 21 Mar. 2004, *J. G. Duckett s.n.* (BBSUK); Slindon, 8 Mar. 2000, *H. W. Matcham s.n.* (BBSUK). SCOTLAND: Glen Falloch, Perthshire, 1799–1871, *W. Wilson s.n.* (MICH).

U.S.A. MAINE: Aroostook Co., Allagash Plantation, 47°06′04″ N, 69°04′31″ W, 23 Jun. 2006, *R. Pursell 12602* (MO), 47°01′40″ N, 69°05′01″ W, 24 Jun. 2006, *B. Allen 27619* (MO); Cumberland Co., Quahog Bay, *s.coll.* (MICH); Franklin Co., Coburn Gore, 45°23′11″ N, 70°46′37″ W, 18 Jun. 2007, *B. Allen 28339* (MO), *R. A. Pursell 12749* (MO), Stetsontown Township, 45°09′30″ N, 70°43′51″ W, 6 Jul. 2008, *B. Allen 29094* (MO), *R. A. Pursell 12857A* (MO); Kennebec Co., Town of Vienna, 44°33′50″ N, 69°59′24″ W, 23 Jun. 2007, *R. A. Pursell 12790* (MO); Knox Co., base of Mt. Megunticook, 26 Aug. 1987, *s.coll.* (MICH); Hancock Co., Mt. Desert Island, 9 Aug. 1908, *E. B. Chamberlain s.n.* (MICH), 27 Aug. 1920, *W. R. Taylor s.n.* (MICH); Piscataquis Co., Schoodic Lake, 11 Aug. 1963, *F. J. Hermann 19126* (MICH); Washington Co., 44.694°N, 67.148°W, 4 Jul. 2008, *B. Shaw 8063* (DUKE). MICHIGAN: Chippewa Co., Sugar Island, Jun. 1933, *W. C. Steere 3323* (MICH), *3500* (MICH); Ernmer Co., Cuil Bay, 7 Aug. 1942, *F. E. Wynne 2755* (MICH); Luce Co., Jul. 1984, *S. L. Planisek s.n.* (MICH); Mackinac Co., 10 Aug. 1968, *H. Crum s.n.* (MICH), 16 Jul. 1939, *I. Schnooberger 2666* (MICH); Marquette Co., 20 Jun. 1971, *F. J. Hermann 23771a* (MICH); Otsego Co., 7 Aug. 1969, *H. Crum s.n.* (MICH). MINNESOTA: Saint Louis Co., Proctor, 30 Jun. 1884, *W. H. 35/2* (MICH). NEW BRUNSWICK: Albert Co., 8 Jul. 1968, *R. R. Ireland 11553* (MICH); Charlotte Co., 6 Jul. 1974, *R. R. Ireland 17063* (MICH); King's Co., 21 Jul. 1970, *R. R. Ireland 13474* (MICH); Madawaska Co., 18 Aug. 1970, *R. R. Ireland 14639* (MICH); Northumberland Co., Mount Carleton Provincial Park, 14 Aug. 1988, *V. N. Bristow & E. Haber s.n.* (MICH); Victoria Co., 10 Jul. 1970, *R. R. Ireland 12855* (MICH); York Co., 13 Jul. 1970, *R. R. Ireland 13028* (MICH). New Hampshire: Cheshire Co., Marlow, Sand Pond, 8 Mar. 1839, *W. S. Allen & L. D. Stair s.n.* (MICH); Lebanon, May 1995, *G. G. Kennedy 774-2* (MICH); White Mountains, Little River, 6 Sep. 1916, *J. Kaisen s.n.-1* (MICH). New York: Adirondack Mt., 13 Sep. 1900, *E. G. Britton s.n.* (MICH), 20 Sep. 1898, *s.n.* (MICH); Buffalo, *s.coll.* (MICH); Catskill Mts., Aug. 1868, *F. T. Cleve s.n.* (H2048027, 2048028); Essex Co., 12 Aug. 1966, *S. J. Smith 40567* (MICH); Hamilton Co., Adirondack Mts., 1 Aug. 1958, *F. J. Hermann 14600* (MICH), 19 Aug. 1957, *13831* (MICH). North Carolina: Highlands, Biological Station, 2 Sep. 1947, *W. C. Steere 10011* (MICH); Jackson Co., 35.16398°N, 83.02696°W, 20 Mar. 2005, *B. Shaw 5268* (DUKE), Blue Ridge Parkway, 20 Sep. 1968, *D. H. Vitt 1345-1* (MICH), *1346-1* (MICH), *1350-1* (MICH), Cedar Cliff Mt., 21 Sep. 1968, *1360-1* (MICH); Macon Co., 3 Sep. 1947, *W. C. Steere 10231* (MICH); Swain Co., 23 Sep. 1968, *D. H. Vitt 1380-1* (MICH); Watauga Co., Dutch Creek valley, 12 Jun. 1978, *J. Rohrer 511b* (MICH). Pennsylvania: Monroe Co., Pocono Mts., 27 Jun. 1893, *E. G. Britton s.n.* (MICH); New England, *s.coll.* (MICH). Vermont: Essex Co., 44.99620° N, 71.69815° W, 19 May 2008, *B. Shaw 7135* (DUKE); Windham Co., Newface Hill, Sep. 1933, *A. J. Grout s.n.* (MICH536809, 536838), Stratton, Pike Hollow, 8 Feb. 1841, *J. Schurberger 4028* (MICH), *4029* (MICH). Virginia: Giles Co., Little Stony Creek, Jun. 1890, *M. Timmerman & Dr. and Mrs. N. L. Britton s.n.* (MICH).

7. **Ulota cochleata** Venturi, Öfvers. Finska Vetensk.-Soc. Förh. 35: 42. 1893. Type: Australia. Tasmania, Mt. Wellington, Springs to Falls, 2 Mar. 1891, *W. A. Weymouth 898* (holotype, TR; isotype, HO!).

Plants ca. 1–1.5 cm tall, yellowish green to green above, brown to black below. Stems usually branched. Leaves strongly twisted or crisped when dry, wide-spreading when moist, (1.5–) 1.9–2.2 (–2.6) mm long; leaf lamina narrow lanceolate, unistratose; leaf base wide, ovate; apex long acuminate; leaf margin plane or slightly partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells round to oblong, (7–) 9–13 (–18) × (4–) 6–8 (–11) μm, thick-walled, with low simple papillose; basal inner cells linear, rectangular to vermicular, (12–) 27–37 (–48) × 1–2 (–3) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in (3–) 4–7 (–11) rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves somewhat longer, (2.6–) 2.7–3 (–3.1) mm. Vaginula not seen. Seta (3–) 4–5.5 (–7) mm long, twisted anticlockwise when dry. Capsule long exserted, (1.4–) 1.5–1.7 (–1.9) mm long. Urn cylindrical, not or slightly, rarely strongly constricted below the mouth when dry and empty, eight ridges if present along the entire length. Neck short, abruptly narrowed to the seta. Exothecial cells differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, confined to the urn. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, variably recurved when dry, sometimes lying on the exothecium, lanceolate, densely and finely papillose on both sides. Endostome segments 8, filiform to linear, often fragile, rarely narrow-lanceolate, as tall as teeth, uniseriate, 1/4–1/6 width of teeth, hyaline, smooth outside, slightly scabrous inside. Opercula yellowish, with a short beak. Calyptra mitrate, densely, rarely sparsely hairy. Spores spherical, finely papillose, (22–) 27–31 (–37) μm in diameter.

Illustration: Figures 41 and 42.

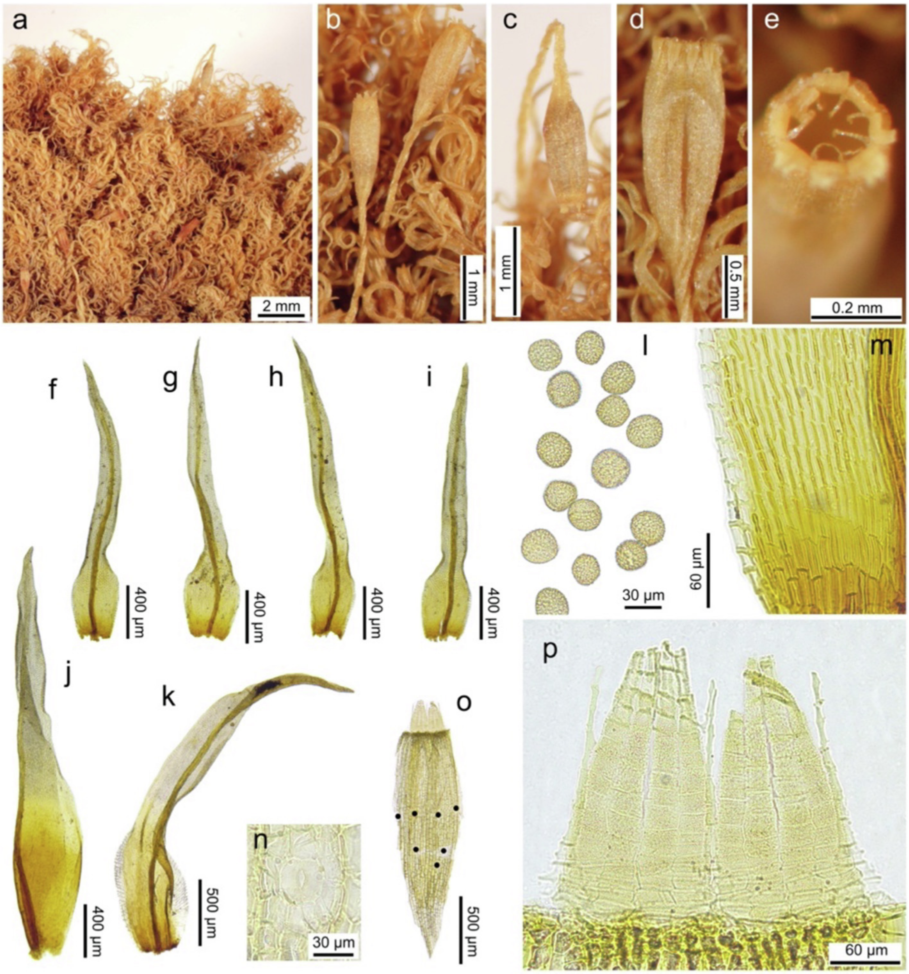


Fig. 41 – *Ulota cochleata* Venturi. a. Habit. b–d. Capsules in dry. e. Capsule mouth viewed from above. f–i. Leaves. j–k. Perichaetial leaves. l. Spores. m. Marginal cells at leaf base. n. Stoma. o. Exothecial wall, with dots indicating stoma position. p. Peristome. (All from isotype in HO except f–i, j and m from *L. Rodway 1524* [non-type, HO]).

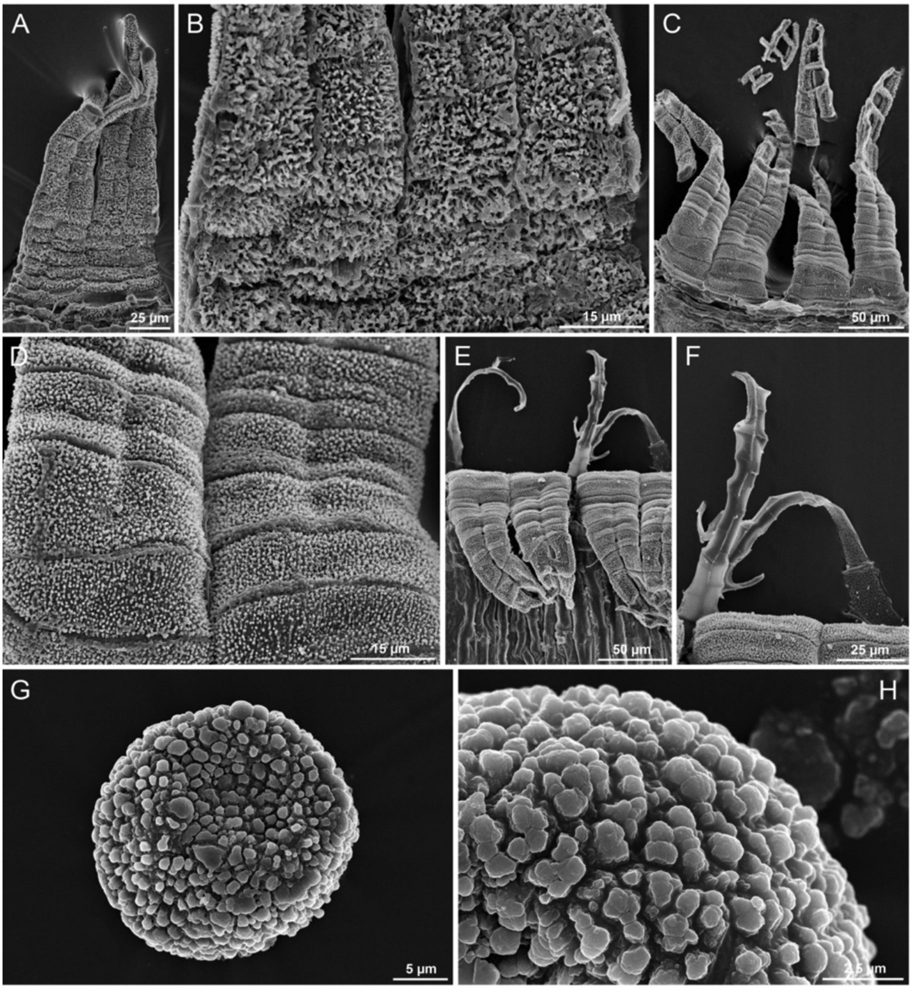


Fig. 42 – *Ulota cochleata* Venturi. A, outer surface of exostome; B, outer surface of basal exostome; C, inner surface of exostome; C, inner surface of basal exostome; E, inner surface of upper exostome; F, outer and inner surface of endostome segments; G, a spore; H, surface ornamentation of a spore. (All from the isotype in HO).

Habitat: It grows on branches, twigs or trunks of trees or shrubs, such as *Cassinia*, *Hymenanthera*, *Lomatia*, *Olearia* and *Tasmannia*, rarely on rocks. There are some records of altitude: (305–) 600–850 (–1200) m. It often occurs with *Ulota crispa* (= *U. lutea*) together.

Distribution: It is **endemic** to Australia and even almost to the island of Tasmania. Figure 43.

Notes: *Ulota cochleata* was reduced as a synonym of *U. viridis* (Streimann and Klazenga, 2002; Streimann and Curnow, 1989), but later resurrected by Ramsay (2006). He (2006) stated that the leaves in *Ulota cochleata* are twisted but not crisped

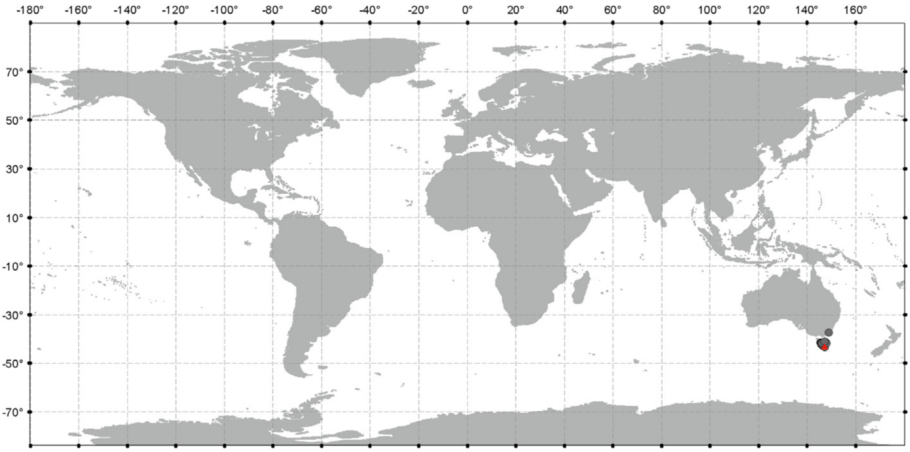


FIG. 43 – Distribution of *Ulota cochleata* worldwide. The red triangle indicates the type locality.

when dry, but we found no significant difference in the dry state of leaves between *U. cochleata* and *U. crispa (=U. lutea)*, for the latter, the leaves are widely considered as crisped.

The main diagnostic characteristics of *Ulota cochleata* contains strongly crisped leaves, hardly or slightly constricted capsules, stomata that occur on the urn, and somewhat filiform endostome segments.

Ulota cochleata locally resembles *U. crispa*, both have crisped leaves, distinctly differentiated cells at the leaf marginal base, cylindrical capsules, and eight narrow endostome segments. However, *Ulota crispa* differs in the strongly constricted capsules, stomata confined to the transition zone between the urn and neck, and narrow but never fragile endostome segments. In Australia, only *Ulota cochleata* has stomata present on the urn. But outside Australia, this character is more common in South America, such as *Ulota fuegiana*. Besides stoma position, it is also similar to *Ulota cochleata* in the capsules, often slightly constricted when dry, fragile endostome segments and stomata restricted to the urn. However, *Ulota fuegiana* is usually distinguished by flexuose leaves and more rows (6–10) of hyaline cells at the leaf marginal base.

Key to *Ulota cochleata* and its closely related species.

1. Stomata occur on the transition zone between urn and neck; endostome segments narrow-lanceolate, never fragile; capsules always moderately to strongly constricted when dry........ *U. crispa*
1. Stomata occur on the urn; endostome segments often filiform to linear, fragile; capsules slightly, sometimes strongly constricted when dry........ 2
2. Leaves usually flexuose when dry; marginal cells at leaf base differentiated in more rows (6–10)........ *U. fuegiana*
2. Leaves strongly twisted or crisped when dry; marginal cells at leaf base differentiated in less rows (4–7)........ *U. cochleata*

Additional Specimens Examined: **Australia**. Tasmania: Betts Track, Wombat Hill, 21 Nov. 1989, *J. Jarman s.n.-2* (HO); Boyd Lookout, 16 Feb. 2000, *J. Jarman s.n.-2* (HO); Central Highlands, 27 Feb. 1990, *A. Moscal 19432* (HO), 16 May 1996, *A. Moscal 28333B* (HO), 11 Oct. 1999, *A. Moscal 30815-1* (HO), 12 Oct. 1999, *A. Moscal 30866* (HO), 29 Mar. 2001, *A. Moscal 31232G* (HO); Cradle Mountain, 21 Nov. 2000, *N. E. Bell 741* (BM); Guy Fawkes Rivulet, 6 Sep. 1890, *W. A. Weymouth 899* (HO); Lady Barron Creek, Mt Field National Park, 7 Dec. 1988, *J. A. Curnow 2604A* (HO); Lomatia Vale, 3 Oct. 2008, *A. M. Gray 1920* (HO); Middlesex Plains, 25 May 2010, *J. Jarman s.n.* (HO); Mt. Wellington near Collin's Bonnet, 15 Jan. 1893, *L. Rodway 1524* (HO); Ringarooma Municipality, on slopes of Mt. Victoria, 24 Nov. 1973, *D. H. Norris 28409* (MICH); South West, Mount Mangana, South Bruny range, 27 Apr. 1993, *A. Moscal 25061-2* (HO); Surprise Valley east of Queenstown, 10 Jul. 1966, *Gillis Een Au153* (S); track from Fish River to Howells Hut, 15 Nov. 1980, *A. V. Ratkowsky s.n.* (HO); Vale of Belvoir, 14 Mar. 2010, *L. H. Cave 1118a* (HO), 16 Mar. 2010, *1215* (HO), *1216-2* (HO); West Coast, Zig Zag Hill, 17 Nov. 1990, *A. Moscal 20214-1* (HO); 2 km SW of Waratah on Corinna Road, 12 May 1997, *R. D. Seppelt 20179* (HO), *20182* (HO), *H. Streimann 59710-1* (HO), *59711* (H). Victoria: Goonmirk Rocks, Errinundra Flora Reserve, 10 Apr. 1986, *H. Streimann 36653* (H).

8. **Ulota crispa** (Hedw.) Brid., Muscol. Recent. Suppl. 4: 112. 1819 [1818]. ≡ *Orthotrichum crispum* Hedw., Sp. Musc. Frond.: 162. 1801. ≡ *Weissia crispa* (Hedw.) Schreb. Ex Gaertn., Meyer & Schreb., Oek. Techn. Fl. Wetterau 3 (2): 94. 1802. ≡ *Ulotrichum crispum* (Hedw.) B.S.G., Bryol. Eur. 3: 1. 1851. (fasc. 46–47. Consp. Vol. 3. I.). nom. illegitimate. Type: "In saxis, arborum truncis per omnem Europam." (lectotype, G, designated by Vitt, 1970).

Bryum striatum S. Linn., Sp. Pl.: 115. 1753.

Neckera ulophylla Web. & Mohr, Bot. Taschenb.: 236. 1807. ≡ *Weissia ulophylla* (Web. & Mohr) Lindb., Musci Scand.: 28. 1879.

Orthotrichum dilatatum Bruch & Schimp., Bryologia Europaea 3: 64. 277 (fasc. 2–3 Mon. 22. 11). 1837.

Orthotrichum pyriforme Opiz, Seznam Rostlin Květeny České 3: 199. 1852.

Orthotrichum ulophyllum Kindb., Bih. Svensk. Vet. Ak. Handl. 7 (9): 121. 1883. nom. illeg.

Ulota bellii Malta, Acta Horti Bot. Univ. Latv. 7: 15. ic. 1933. Type: New Zealand. "Lake Harris", Feb. 1895, *W. Bell* (holotype, H4337019!). Proposed by Fife (2017).

Ulota bellii var. *longicolla Malta*, Acta Horti Bot. Univ. Latv. 7: 16 (1933) Type: New Zealand. South Island, Jan. 1902, *R. Brown s.n.* (isotype, WELT-M005751). Proposed by Fife (2017).

Ulota breviseta Malta, Acta Horti Bot. Univ. Latv. 7: 9. 1933. Type: New Zealand. Mt. Maungatua, Jan. 1888, *W. Bell* (lectotype, H4337011! designated by Fife, 2017); North Island, Hawkes Bay, no bark of small trees near Lake Waikaremoana, ca. 2300', 28 Dec. 1932, *Sainsbury* (paralectotype, BM000919964!). Proposed by Fife (2017).

Ulota camptopoda Kindberg in Macoun, Catalogue of Canadian Plants, Part VI, Musci: 85. 1892. Type: Canada. Quebec, cemetery W of Hull, Aylmer Road, 26 Apr. 1891, *J. Macoun 582* (lectotype, FH00059347! designated here; isolectotypes, CANM! FH00059346! FH00059348!).

Ulota cervina Hoe & H.A. Crum, Bryologist 74: 487. f. 10–13. 1971[1972]. Type: U.S.A. Hawaii, Maui, Kipahulu Valley, abundant as small cushions, more or less exposed, usually on older portions of various stems and branches, ohia (Metrosideros) forest, vicinity of Base Camp no.3, ca. 6375 ft. elev., 28 Aug. 1967, *W. J. Hoe 1803.0* (holotype, MICH526539! S-B181071!).

Ulota connectens (Kindb.) Kindb., Enumeratio Bryinearum Exoticarum, supplementum 2: 108. 1891. ≡ *Orthotrichum connectens* Kindb., Ottawa Naturalist 3: 150. 1890. Type: Canada. Ontario, Dow's Swamp, near Ottawa, *Macoun* (syntypes, CANM, NY).

Ulota crispa var. *norvegica* (Gronvall) A.J.E. Sm. & M.O. Hill, Journal of Bryology 8: 431. 1975.

Ulota crispula var. *dolosa* Renauld & Cardot, Botanical Gazette 22: 51. 1896. Type: U.S.A. District of Columbia, Tenallytown, 1892, *J. M. Holzinger* (type, FH00220826!).

Ulota fulva Brid., Bryol. Univ. 1: 301. 1826. Type: France. Réunion, "in insulae Borboniae arboribus caespitose habitat, Bory St. Vincent detexit." (lectotype, PC0098900! designated by Wang and Jia, 2012b; isolectotype, BM!).

Ulota longifolia Dixon & Sakurai, Bot. Mag. (Tokyo) 49: 140. 1935. Type: Japan. Hondo, Prov. Sagami, Hakone-pass, Aug. 1910, *K. Sakurai 193* (not located).

Ulota lutea (Mitt.) Mitt., J. Proc. Linn. Soc. Bot. 4: 77. 1859. ≡ *Orthotrichum luteum* Mitt. in Wilson in Hook.f., Flora Tasmaniae 2: 184. 1859. Type: Australia. Tasmania, Western Mountains, rivulet behind Cumming's Head, on trees, *Archer* (lectotype, NY01202141! designated by Wang and Jia, 2012b; isolectotype, BM000825450!).

Ulota macrocarpa Broth., Symb. Sin. 4: 70. 1929. Type: China. Hunan, Prope urbem Wukang, in silva frondosa elata umbrosa montis Yün-schan, ad arbores, alt. 1200–1300 m, 8 Aug. 1917, *Dr. Heinr. Frh. v. Handel-Mazzetti (Diar. Nr. 2206)*, (lectotype, H4335024! designated by Guo *et al.*, 2004); Sichuan, Huili, Lungdschu-schan (Mt. Longzhou), "an Bambushalmen", 3000–3675 m, 26 Mar. 1914, *Dr. Heinr. Frh. v. Handel-Mazzetti 820* (isosyntype, S!).

Ulota ulophylla Broth., Die Natürlichen Pflanzenfamilien I (3): 473. 1902.

Ulota ulophylla subsp. *eu-ulophylla* Giacom., Istituto Botanico della R. Università R. Laboratorio Crittogamico Pavia, Atti 4: 249. 1947. *nom. illegitimate.*

Ulota weymouthii Venturi, Pap. & Proc. Roy. Soc. Tasmania 1912: 114. 1913. Type: Australia. Tasmania, Mt. Wellington (not located).

Plants 0.5–2.5 cm tall, yellowish green to green above, brown to black below. Stems usually branched. Leaves strongly crisped when dry, wide-spreading, erect-spreading to patent when moist, (1.5–) 2.1–2.6 (–3.2) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex long acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (5–) 9–11 (–15) × (6–) 8–10 (–14) μm, thick-walled, smooth or with low simple papillae; basal inner cells linear, elongate-rectangular to vermicular, (18–) 27–40 (–59) × (2–) 4–6 (–9) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in (3–) 5–11 (–14), hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves somewhat longer, (1–) 1.8–2.9 (–3.3) mm. Vaginula naked or hairy. Seta (1.5–) 3–5 (–7.5) mm long, often twisted anticlockwise when dry. Capsule short to long exserted, (1.3–) 1.4–2.2 mm long. Urn cylindrical to long-cylindrical, moderately to strongly constricted below mouth when dry and empty, eight furrows along the entire length. Neck short, abruptly to gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands near the mouth, ca. four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the base of the urn or on the transition zone between the urn and neck. Preperistome rarely seen. Peristome double. Exostome teeth 16, often united into 8 pairs, lanceolate, recurved when dry, often lying on the exothecium, densely papillose on the outside, striate to papillose above, and obscurely striate below on the inside. Endostome segments 8, rarely up to 16, narrow-lanceolate, as tall as teeth, uni or biseriate, 1/2–1/4 width of teeth, hyaline, smooth outside, slightly scabrous to nearly smooth inside. Opercula with a beak, short to long. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (15–) 19–25 (–34) μm in diameter.

Illustration: Malta (1933), Nyholm (1960), Hoe and Crum (1971), Smith (1978), Crum and Anderson (1981), Ireland (1982), Noguchi and Iwatsuki (1989), Ignatov and Ochyra (1994), Vitt (2014) and Wang and Jia (2012b, 2016); figure 44.

Habitat: It often grows on branches or trunks of trees. There are some records of altitude: 110–1100 m.

Distribution: It is common in North Hemisphere and also occurs in some regions of the South Hemisphere, including Australia, Chile, New Zealand, and Réunion. Figure 45.

Notes: *Ulota crispa* is the most common species in the genus and has been studied a lot in the past. But it is also a species with the greatest variation and thus easily confused with some related species, such as *Ulota bruchii*.

Recently, Caparrós *et al.* (2016) reassessed a complex of *Ulota crispa* and suggested a narrower sense of this species. More comments on their work are under the *Ulota crispula*. According to Caparrós *et al.*'s (2016) and our present works, *Ulota crispa* (s.str. for the whole book unless noted) has the typical morphology of the genus, including strongly crisped leaves, markedly differentiated basal marginal leaf cells, cylindrical capsule strongly contracted below the mouth when dry, simply ornamented exostome, eight well-developed linear endostome, stomata restricted to the urn base or the transition zone between urn and neck and densely hairy calyptra.

In the recent phylogenetic study (Wang *et al.*, 2021), *Ulota lutea* did not form a monophyletic group with *U. crispa*, but we temporarily accept the previous treatment (Wang and Jia, 2012b) here due to their obscure delimitations in morphology which may be clarified in future works.

Suzuki and Iwatsuki (2013) reinstated the species rank of *Ulota longifolia* from synonyms of *U. crispa* based on its longer exostome teeth (325–360 μm *vs.* ca. 300 μm) and 16 papillose narrower endostome segments (uniseriate *vs.* biseriate). However, the authors seem to fail to study the type material, and therefore, their treatment still needs to be confirmed by further study.

Ulota crispa is most easily confused with *U. bruchii*, *U. crispula*, and *U. intermedia*. But *Ulota bruchii* differs in the long-narrowed capsule neck and the distinct striate on the lower half of endostome segments. According to Caparrós *et al.* (2016), *Ulota crispula* can be distinguished by the slightly or moderately crisped leaves, fewer rows (4–9) of hyaline cells at leaf basal margins, capsules that are not or weakly constructed when dry and empty, urns tending to be short-cylindrical in shape and linear, slender endostome segments with thin cross-walls on the inside surface. Further, *Ulota intermedia* can be separated primarily by capsules that are not or are weakly constructed when dry and empty and linear-lanceolate endostome segments with distinctly thickened and prominent cross-walls on the inside surface. However, these differences are not perfect in use according to our study and still need to be studied in the future.

Besides that, there are some other species closely related to *Ulota crispa*, such as *U. calvescens* from Europe, *U. obtusiuscula* from North America and *U. germana* from South America. *Ulota crispa* resembles *U. calvescens* in the strongly crisped leaves, distinctly differentiated leaf-base marginal cells, long exserted capsules, and eight narrow endostome segments. *Ulota calvescens* differs, however, in the less rows (3–6) of hyaline cells at leaf basal margins, the presence of elongated cells inside the leaf margin above the basal part, markedly striate on the inner surface of exostome teeth and sparsely hairy calyptra. Additionally, *Ulota crispa* is similar to *U. obtusiuscula* in having strongly crisped leaves, distinctly differentiated cells at basal leaf margins, long exserted capsules, eight narrow endostome segments, and densely hairy calyptra. But *Ulota obtusiuscula* is easily distinguished by the relatively larger plants (1–3.5 cm), less rows (3–7) of hyaline cells at basal leaf margins, capsules hardly or slightly contracted below the mouth and usually with several layers of red or orange cells near the mouth, and relatively longer seta (5–7.5 mm). Furthermore, *Ulota crispa* also shares many characters with *U. germana*, including strongly crisped leaves, conspicuously differentiated basal marginal leaf cells, often strongly constricted capsules, stomata located at the basal part of capsules, eight narrow endostome segments, and densely hairy calyptra. However, *Ulota germana* differs in the shorter seta (1.7–2.9 mm), remarkably longer perichaetial leaves (2.8–3.4 mm) that often sheathing the seta, shorter capsules (1–1.2 mm), and larger spores (32–35 μm).

In a broad sense, *Ulota crispa* is undoubtedly the species with the largest variation in the genus. This is probably correlated to its rather wide geographical distribution in the world. We consider that its wider distribution makes *Ulota crispa* live in many different microenvironments so that in the process of evolution, it tends to vary in morphology in order to adapt to these different microenvironments. But this process is still in progress, and thus these variations are not significant. The variation of *Ulota crispa* is mainly in the degree of leaf crispness when dry, the degree of differentiation of leaf basal marginal cells, the shape of capsules, the degree of constriction of dry capsules, and the number, shape and ornamentation of endostome segments.

Key to *Ulota crispa* and its closely related species.

1. Capsules moderately to strongly constricted below the mouth when dry and empty........................2
1. Capsules hardly or slightly constricted below the mouth when dry and empty........................5
2. Perichaetial leaves often prominently sheathing the seta; seta shorter, 1.7–2.9 mm; capsules shorter, 1–1.2 mm; spores large, 32–35 µm................*U. germana*
2. Perichaetial leaves not prominently sheathing the seta; seta longer, 3–5.5 mm; capsules longer, 1.4–2.8 mm; spores relatively smaller, 19–25 µm....................3
3. Leaf cells inside margin above the basal part becoming elongate in a few rows, forming a band ascending the margin and reaching to mid-leaf; exostome teeth prominently striate on the inside surface; calyptra often sparsely hairy ....*U. calvescens*
3. Leaf cells above the basal part almost uniform; exostome teeth papillose-striate to obscurely striate on the inside surface; calyptra densely hairy......................4
4. Capsules with long neck when dry and empty; endostome segments often with longitudinally striolate at the base........................*U. bruchii*
4. Capsules with short neck when dry and empty; endostome segments often scabrous to nearly smooth at the base........................*U. crispa*
5. Plant relatively larger, 1–3.5 cm; capsules often becoming red or orange in several layer of cells around mouth; seta longer, 5–7.5 mm; endostome segments relatively wider, narrow-lanceolate........................*U. obtusiuscula*
5. Plant smaller, 1–2.5 cm; capsules never becoming red or orange in several layer of cells around mouth; seta relatively shorter, 2–4 mm; endostome segments narrower, linear to linear-lanceolate........................6
6. Leaves flexuous, slightly to moderately crisped when dry; endostome segments linear, slender and fragile, often with thin cross-walls on the inside ....*U. crispula*
6. Leaves strongly crisped when dry; endostome segments linear to linear-lanceolate, not fragile, often with distinctly thickened and prominent cross-walls on the inside........................*U. intermedia*

Additional specimens examined: **Australia**. TASMANIA: Hobart Rivulet, 147°19′ E, 42°54′ S, 4 Dec. 1897, *W. A. Weymouth 2508* (HO), *2510* (HO); Mt. Wellington, 26 Dec. 1887, *W. A. Weymouth 1534* (HO), 28 Dec. 1897, *s.n.* (HO), 2 Jan. 1894, *s.n.-1* (HO); Recherche Bay, 17 Jan. 1911, *W. A. Weymouth 2488* (HO), *2489* (HO), *2923* (HO).

Austria. BURGENLAND: Güssing, 2 May 1959, *J. Froehlich s.n.* (S). CARINTHIA: 28 Jul. 1956, *J. Froehlich s.n.* (S). OBERÖSTERREICH (UPPER AUSTRIA): Goisern, 21 Jul. 1955, *J. Froehlich s.n.* (S), 18 Aug. 1962, *s.n.* (S); Langbathseen, 23 Jul. 1953, *J. Froehlich s.n.* (S); Obertraun, *s.coll.* (S). SALZBURG: Bad Gastein, 19 Jul. 1952, *J. Froehlich s.n.* (S); Pinzgau, Jul. 1879, *J. Briedler* (S). TYROL: s. loc., 1860, *M. Hutt s.n.* (H).

Belarus and Poland. GRODNO AND BREST: Puszcza Bialowieska, 24 Apr. 1958, *S. Lisowski s.n.* (H).

Canada. BRITISH COLUMBIA: Calvert Island, 51°40′ N, 128°08′ W, 18–20 Jun. 1965, *W. B. Schofield 26899* (UBC), *27071* (UBC); Dawson's Landing, 51°35′ N, 127°40′ W, 2 Aug. 1986, *W. B. Schofield 85988-3* (UBC); Lewis Island, 54° N, 130° W, 25 Jun. 1979, *W. B. Schofield, D. H. Vitt & D. Horton 72913* (UBC); Mt. Buxton, 10 Aug. 1965, *W. B. Schofield 27825* (UBC); Namu Lake, 51°51′ N, 127°51′ W, 4 Aug. 1986, *W. B. Schofield 86158-1* (UBC), *86158-2* (DUKE); s. loc., 10 Aug. 1965, *W. B. Schofield 27798-2* (DUKE); Queen Charlotte Islands, 27 Aug. 1961, *W. B. Schofield 15726* (UBC), 53°50′ N, 132°09′ W, 18 Jun. 2002, *119616* (UBC); Skeena River, near Kwinitsa, 11 Jun. 1963, *W. B. Schofield 21003* (UBC); Vancouver Island, 24 Jul. 1977, *Dull s.n.* (H), 49°15′ N, 123°11′ W, 19 Jul. 2004, *W. B. Schofield 123009* (UBC), Ucluelet, 11 May 1909, *J. Macoun s.n.* (MICH539711, 539712); Victoria, 10 Jun. 1908, *J. Macoun s.n.* (MICH). NEW BRUNSWICK: Albert Co., 45°39′ N, 65°02′ W, 1 Sep. 1967, *R. R. Ireland 10721* (MICH), Fundy National Park, 45°35′ N, 64°59′ W, 8 Jul. 1968, *R. R. Ireland 11547* (H, MICH), 45°38′ N, 65° 00′ W, 7 Jul. 1968, *11520* (MICH); BullPasture Plain, 7 Jul. 1981, *S. Woods 10695* (MICH); Kent Co., 46°38′ N, 64°57′ W, 6 Aug. 1970, *R. R. Ireland 14197* (MICH), *14199* (MICH); Victoria Co., 46°38′ N, 67°42′ W, 9 Jul. 1970, *12789* (MICH). NEWFOUNDLAND: Avalon Peninsula, 16 Jun. 1975, *A. J. Fife 915* (H), Sep. 1971, *J. A. Hancock 52* (H), Holyrood, 1 Jun. 1956, *T. Ahti s.n.* (H), 47°22′ N, 53°10′ W, 11 Jun. 1949, *R. Tuomikoski 753* (H), Deep Bight, 48°06′ N, 53°57′ W, 21 Jun. 2002, *W. B. Schofield 119529* (DUKE, UBC); Bonavista North Distr., 17 May 1972, *G. R. Brassard 7031* (H); Burgeo-La Poile, 47°41′ N, 56°34′ W, 21 Jun. 1949, *R. Tuomikoski 1345b* (H); Cape Ray, 47°37′ N, 59°10′ W, 29 Jun. 1949, *R. Tuomikoski 1905* (H); Ferryland Distr., 46°44′ N, 53°17′ W, 7 Jun. 1949, *R. Tuomikoski 352* (H), *426* (H, MICH), 3 Jun. 1956, *T. Ahti 9645* (H); Gambo, 48°43′ N, 54°18′ W, 26–27 Aug. 1949, *R. Tuomikoski 4905* (H); Grand Falls Distr., 18 Jul. 1956, *T. Ahti 8095* (H), 26 Jul. 1956, *8464* (H); Gander Lake, 48°52′ N, 54°40′ W, 2 Sep. 1949, *R. Tuomikoski 6089* (H), 2 Aug. 1956, *T. Ahti 8628* (H), 48°53′ N, 54°24′ W, 20 Oct. 1975, *G. R. Brassard 10516* (H, MICH); Gaultois, Fortune Bay and Hermitage, 47° 34′ N, 55°56′ W, 26 Jun. 1949, *R. Tuomikoski 1726* (H); Gros Morne National Park, 49°22′ N, 57°59′ W, 11 Sep. 1980, *R. J. Belland 3912-2* (MICH); Gros Morne, 49°35′ N, 58°47′ W, 3 Aug. 1987, *W. B. Schofield 89347* (UBC); Humber, 48°58′ N, 58°16′ W, 15 Aug. 1949, *R. Tuomikoski 5335* (H); Humber East Distr., 13 Jun. 1956, *T. Ahti 8088* (H), 23 Jun. 1956, *8740* (H); Placentia Bay, 7 Jun. 1972, *J. A. Hancock 234* (MICH); Placentia west Distr., 23 Aug. 1956, *T. Ahti 6467* (H), *9189* (H); Pushthrough Fortune Bay and Hermitage, 47°36′ N, 56°10′ W, 23–24 Jun. 1949, *R. Tuomikoski 1494* (H), *1542* (H), *1543* (H), *1545* (H); St. Alban's, Fortune Bay and Hermitage, 26 Jun. 1949, *R. Tuomikoski 1784a* (H); St. Barbe, 50°42′ N, 57°11′ W, 28 Jul–2 Aug. 1949, *R. Tuomikoski 4448* (H), 50°42′ N, 57°05′ W, 31 Jul. 1949, *R. Tuomikoski 4572* (H), *4583* (H), 49°52′ N, 57°54′ W, 10 Aug. 1949, *R. Tuomikoski 5019* (H), 49°50′ N, 57°52′ W, 11 Aug. 1949, *R. Tuomikoski 5217* (H), 49°54′ N, 57° 50′ W, 7–13 Aug. 1949, *5123* (H, MICH); St. Geogore's Distr., 7 Jul. 1956, *T. Ahti*

7417 (H), 5 Jul. 1956, *7644* (H), *9819* (H); St. George's-Port au Port, 48°30′ N, 58° 19′ W, 5–6 Jul. 1949, *R. Tuomikoski 2204* (H, MICH), *2215* (H), *2563* (H), *2798b* (H); St. Mary's Distr., 6 Jun. 1956, *T. Ahti 8670* (H); Trinity North Distr., 5 Sep. 1956, *T. Ahti 8141* (H); White Bay, Hampden, 49°28′ N, 56°49′ W, 12 Jul. 1949, *R. Tuomikoski 3072* (H). Nova Scotia: Anapolis Co., 44°29′ N, 65°08′ W, 3 Aug. 1968, *R. R. Ireland 12520* (MICH), *12537* (H); Colchester Co., 45°28′ N, 64°06′ W, 12 Jul. 1974, *R. R. Ireland 17376* (H, MICH); Cumberland Co., 45°21′ N, 64°49′ W, 15 May 2004, *T. Ahti 62555b* (H), 45°38′ N, 63°33′ W, 7 Sep. 1967, *R. R. Ireland 10676* (MICH); Kings Co., 22 Jul. 1965, *W. B. Schofield 27494-1* (UBC), 4 Oct. 1996, *106594* (DUKE, UBC); Halifax Co., 5 Jul. 1929, *L. E. Wehmeyer 1095* (MICH536785, 536799, 536906), 44°45′ N, 63°18′ W, 24 Jul. 1968, *R. R. Ireland 12131* (MICH), 44°55′37.1″ N, 62°32′45.3″ W, 5 Oct. 2005, *R. M. King & R. M. Garvey B616* (DUKE); Inverness Co., 46°43′ N, 60°55′ W, 21 Jul. 1968, *R. R. Ireland 12047* (MICH), 46°49′ N, 60°46′ W, 23 Jun. 1988, *W. B. Schofield & R. J. Belland 91607-1* (UBC); Richmond Co., Cape Breton Island, 25 Jun. 1984, *D. H. Vitt 31263* (MICH); Shelburne Co., 28 Jul. 1968, *R. R. Ireland 12234* (MICH), 29 Jul. 1968, *12325* (MICH), 30 Jul. 1968, *12364* (MICH); Truro, *s.coll.* (MICH); Victoria Co., 6 Sep. 1967, *R. R. Ireland 10685* (MICH), 14 Jul. 1968, *11779* (MICH), 12 Jul. 1988, *W. B. Schofield & R. J. Belland* 92613 (H); Yarmouth Co., 28 Aug. 1922, *W. R. Taylor s.n.* (MICH536899, 536904), 44°00′ N, 66°04′ W, 31 Jul. 1968, *R. R. Ireland 12401* (MICH). Ontario: Algonquin Park, Norway Lake, 30 Aug. 1939, *R. F. Cain 2319* (H), Brewer Lake, 5 Sep. 1939, *R. F. Cain s.n.* (MICH); Hastings Co., 45°25′ N, 77°45′ W, 1 Jun. 1972, *R. R. Ireland 15912* (MICH), 44°40′ N, 77°29′ W, 5 Jul. 1972, *R. R. Ireland 16253* (H); Lake Superior, *s.coll.* (H); Middleset Co., 31 May 1949, *W. M. Stewart 589* (MICH); Muskoka, 45°18′ N, 79°22′ W, 25 Jul. 1987, *R. R. Ireland 22992* (MICH); s. loc., 1889, *J. Macoun 312* (DUKE); Ottawa, *s.coll.* (MICH); Parry Sound Distr., 45°21′ N, 80°02′ W, 21 Jul. 1982, *R. R. Ireland 20706* (H, MICH), 45°30′ N, 79°55′ W, 9 Sep. 1989, *24120* (H, MICH), 45°26′ N, 79°35′ W, 24 Jul. 1986, *22065* (MICH); Peel Co., 16 Oct. 1948, *R. F. Cain 3475* (H); Sprucedale, 45°30′ N, 79°27′ W, 25 Jul. 1987, *R. R. Ireland 23027* (H). Prince Edward Island: King Co., 29 Jul. 1970, *13896* (MICH), 46°27′ N, 62°16′ W, 1 Aug. 1970, *14060* (H, MICH), 2 Aug. 1970, *14068* (H, MICH), 2 Sep. 1967, *10173* (MICH); s. loc., 2 Jul. 1888, *J. Macoun s.n.-2* (MICH); Queens Co., 24 Jul. 1970, *R. R. Ireland 13569* (H, MICH), 25 Jul. 1970, *13663* (H, MICH), 27 Jul. 1970, *13800* (MICH), 28 Jul. 1970, *13824* (MICH). Quebec: Gaspe Est, 25 Jul. 1960, *H. Crum & H. Williams 10884* (H, MICH); south of Sainte-Anne-des-Monts, 29 Aug. 1967, *R. R. Ireland 11156* (MICH).

Chile. Los Ríos: Valdivia, *W. Lechler s.n.* (H). Magallanes y Antártica Chilena: Sarmiento Channel, 7 Jun. 1882, *Mall* (MICH).

China. Chongqing: Chengkou Co., 31°51.207′ N, 109°07.520′ E, 6 Jul. 2008, *Y. Jia 10129* (PE); Jinfo Mt., 9 Apr. 1935, *P.-C. Chen 1493c* (PE), 20 Aug. 1987, *X.-Y. Hu 0721a* (PE); Shizhu Co., Huangshuizhen, 30°10.245 N, 108°23.885 E, 15 Jul. 2008, *N.-N. Yu 01629* (PE), *01630* (PE), *01631* (PE), 30°15.36′ N, 108°26.60′ E, 17 Jul. 2008, *N.-N. Yu 01832* (PE), 18 Jul. 2008, *01959* (PE); Wushan Co., 31°25.042′ N, 109°58.585′ E, 11 May 2008, *Y. Jia 10096* (PE), Wulipo, 31°36.508′ N, 109° 91.767′ E, 8 May 2008, *Y. Jia 10042* (PE), 31°23.960 N, 110°01.227 E, 11 May 2008, *Q.-H. Wang 952* (PE), Dengjiaxiang, 30°49.59′ N, 110°01.41′ E, 9 Sep. 2009, *L.-J. Zhao Z948* (PE). Fujian: Wuyi Mt., 20 Apr. 1955, *Bryophyte training class 933-a* (PE). Gansu: Wen Co., Qiujiaba, 32°54.982′ N, 104°18.503′ E, 20 May 2007, *Y. Jia 09267* (PE). Guangxi: Tianlin Co., Cenwang Laoshan National Nature Reserve, 22 Aug. 2019, *Y.-M. Wei et al. 190822-40* (IBK); Leye Co., Yachang Orchidaceae National Nature Reserve, 2 Oct. 2018, *Q.-M. Tang & S.-Y. Zhang 20181002-341* (IBK). Guizhou: Daozhen Co., 3 Aug. 2003, *Q. He 269* (PE), *Y.-Q. Huang 235* (PE), *281* (PE), 3 Aug. 2003, *M.-Z. Wang 59117* (PE), *59152* (PE), *59141* (PE); Jiangkou Co., Fanjing Mt., 29 Jul. 1983, *Q. Gao & J.-Y. Feng 32607-2* (IFP), 25 Aug. 2000, *M.-Z. Wang 56015* (PE), *Q. Gao 32346* (PE); Suiyang Co., Kuankuoshui, 11 Nov. 1991, *P.-C. Wu 24102* (PE). Heilongjiang: Hailin Co., Changbai Mt., 28 Aug. 1973, Q. Gao & G.-C. Zhang 3168 (IFP). Hubei: Shennongjia, Jun. 1976, *P.-C. Wu 347-c* (PE), 9 Jul. 1996, *P.-C. Wu 394* (PE); Xingshan Co., Longmenhe, 8 Oct. 1996, *J.-X. Luo 960721* (PE); Yichang, Dalaoling National Forest Park, 31°03.225′ N, 110° 54.879′ E, 8 Nov. 2007, *Q.-H. Wang 600* (PE), 31°05.13′ N, 110°55.19′ E, 21 Nov. 2008, *Q.-H. Wang 976* (PE). Hunan: Sangzhi Co., Badagongshan National Reserve, 4 Oct. 1998, *T. Koponen, S. Huttunen, S. Piippo & P.-C. Rao 50035* (H), 29°48′ N, 110°07′ E, 6 Oct. 1998, *T. Koponen, S. Huttunen, S. Piippo & P.-C. Rao 50385* (H), *54537* (H), *54616* (H), 7 Oct. 1998, *50495* (H), *54771b* (H), *54782a* (H), *55711* (H3213199, 3213507), 13 Oct. 1998, *57173* (H), 25 Sep. 1999, *P.-C. Rao 58630* (H), 29°47′ N, 110°05′ E, 26 Sep. 1999, *P.-C. Rao 58719* (H), 29 Sep. 1999, *59088* (H), *59091* (H), *59106* (H), 26 Nov. 1999, *58746a* (H), 19 Sep. 2000, *J. Enroth 64611* (H), *64625* (H), 29°47′ N, 110°06′ E, 20 Sep. 2000, *64888* (H), *64897* (H), *64898* (PE), *64902* (H), *64905* (H), *64909* (H), *64921* (H), *64926* (H), *64934* (H), *65024* (H), *V. Virtanen 61268* (H), *61285* (H), *61292* (H), *61312* (H, PE), 21 Sep. 2000, *V. Virtanen 61419* (H), 22 Sep. 2000, *V. Virtanen 61383* (H), *61434* (H), 24 Sep. 2000, *64679* (H), *64731* (H), *V. Virtanen 61236* (H), *61254* (H), *61538* (H); Shimen Co., Hupingshan, 30°01′ N, 110°33′ E, 30 Sep. 1998, *T. Koponen, S. Huttunen, S. Piippo & P.-C. Rao 54087* (H); Yanling Co., Taoyuandong, 26°29′ N, 114°01′ E, 11 Oct. 1998, *T. Koponen, S. Huttunen, S. Piippo & P.-C. Rao 55104* (H), 12 Oct. 1998, *55238* (H), 26°30′ N, 114°04′ E, 13 Oct. 1998, *57173* (PE); Yizhang Co., Mt. Mangshan, 24°55′ N, 112°59′ E, 1 Oct. 1997, *T. Koponen, S. Huttunen & P.-C. Rao 49488* (H). Jilin: Changbai Mt., 6 Jul. 1979, *T. Cao & B.-Y. Yan 397* (IFP). Jiangxi: Lu Mt., 21 Oct. 1982, *Wuhanshiyuan Yang 32996* (IFP). Jilin: Changbai Mt., Longtanshan, *Q. Gao* (PE). Sichuan: Dujiangyan, 13 Jul. 1993, *M.-Z. Wang 49932a* (PE), 24 May 2002, *57525* (PE); Emei Mt., Leiyinsi, 16 Oct. 1942, *C.-L. Yang 7137* (PE), Apr. 1956, *J.-L. Yang 56033* (PE), *Y.-X. Xiao M00033* (PE), Tianmenshi, 25 Aug. 1942, *P.-C. Chen 5558-2* (PE), Jinding, 25 Aug. 1942, *P.-C. Chen 5566* (PE), *5619a* (PE), *5619c* (PE), *5584* (PE), 25 Aug. 1978, *Q. Li 2404* (PE), 11 Aug. 1939, *L.-Y. Dai T117* (PE), *T117-B* (PE), *T206* (PE), s. date, *Q. Gao 18837* (PE00645487, 00645493); Leibo Co., 23 Sep. 1942, *P.-C. Chen 5850* (PE); Nanjiang Co., 32°40.60′ N, 106°59.54′ E, 13 Jul. 2011, *Y. Jia 12170* (PE); Miyi Co., 7 Jul. 1983, *M.-Z. Wang 21142* (PE); Mianning Co., 28°56.283′ N, 102°06.268′ E, 10 Jul. 2005, *Y. Jia 08241* (PE), *08248* (PE), *08250* (PE); Tianquan Co., 6 May 1977, *Q. Li 977* (PE), *982* (PE), 11 May 1980, *J.-X. Luo & B.-D. Xin 910* (PE01755592); Wangcang Co., 32°39′30″ N, 106°32′60″ E, 29 Jun. 2011, *S.-J. Li 107* (PE), *Y. Jia*

12023 (PE), 32°40′14″ N, 106°33′06″ E, 1 Jul. 2011, *S.-J. Li 212* (PE); Wenchuan Co., 23 Aug. 2002, *Y. Jia 07056* (PE), 31°24′13″ N, 103°35′55″ E, 26 Aug. 2002, *Y. Liu 615* (PE), *621* (PE), 27 Aug. 2002, *Y. Jia 06671-c* (PE). Taiwan: Mt. Taiheizan, 28 Mar. 1930, *S. Suzuki s.n.* (H); Nantou Co., Mt. Yu, Nov. 1997, *J.-R. Chen 97467* (PE); Tainan, *M. Tagawa s.n.* (KYO); Taizhong Co., 18 Oct. 1998, *Q. Gao* & *T. Cao 980200* (IFP). Xizang: Milin, Deyang river, 19 Jul. 1983, *Y.-G. Su 5280* (KUN), 21 Jul. 1983, *5311* (KUN); Motuo Co., 19 Aug. 1980, *M.-Z. Wang 800713* (PE). Yunnan: Fugong Co., west slope of Biluoxueshan, 1982, *M.-Z. Wang 7054-a* (PE); Gongshan Co., Dulongjiang, 11 Oct. 1935, *C.-W. Wang 6817* (PE), 3 Sep. 1982, *M.-Z. Wang 11507-a* (PE), May 1979, *A.-L. Zhang 31(a)* (KUN), Gaoligongshan Range, 27°47′38.4″ N, 98°30′29″ E, 4 Oct. 2002, *J. R. Shevock 23366-1* (E); Lijiang Co., 30 Jul. 1985, *X.-J. Li 850137* (PE); Weixi Co., Kangpu, 15 Jul. 1934, *C.-W. Wang 04419* (PE), Biluo Mt., 10 May 1982, *M.-Z. Wang 5849* (PE), 20 May 1982, *4834-b* (PE), 23 May 1982, *6264-a* (PE), Weideng, 20 May 1982, *D.-C. Zhang 434* (KUN, PE), 24 May 1982, *M.-Z. Wang 6369* (PE), *6373-a* (PE), *6395-b* (PE); Yiliang Co., Chaotianma, 17 Sep. 1972, *X.-J. Li 4474* (KUN).

Czech Republic. Hradec Králové: Orlické hory Mts., valley of Divoká Orlice river, 20 Apr. 1996, *B. Buryová 5247* (DUKE). Karlovy Vary: Erzgebirge, Jul. 1934, *A. Kopsch s.n.* (HBG). Moravian-Silesian: Mts. Beskydy, Mt. Smrk, 23 Apr. 1950, *J. Duda s.n.* (MICH).

Denmark. Capital region: Bornholm, *coll. 23* (illegible handwritten name) (H); Copenhagen, 4 Aug. 1902, *A. Hesselbo s.n.* (H). Central region: Himmelbjerget, 2 Oct. 1884, *C. Jensen s.n.* (H). Southern region: Jutland, Sep. 1884, *C. Jensen s.n.* (H). Zealand region: Zealand, 27 Oct. 1901, *C. Jensen s.n.* (H).

Estonia. Harju: Kreis Harrien, Aug. 1911, *E. Niclasen s.n.* (H3150651, 3150652). Pärnu: Kreis Pernau, May 1897, *J. Treboux 473a* (H), *s.n.* (H), 8 Aug. 1909, *J. Mikutowicz 25311* (H). Rapla: Saksa, 31 Jul. 1880, *coll.* (illegible handwritten name) (H). Saare: Abruka, 16 Apr. 1935, *V. Kujala s.n.* (H); Kuresaare, 14 Jun. 1935, *R. Tuomikoski s.n.* (H).

Finland. Åland: Nåtö, Lemland, 23 Jun. 1901, *A. Palmgren s.n.* (H), 13 Jun. 1902, *F. W. Klingstedt s.n.* (H); Ytternäs, 27 May 1961, *H. Roivainen s.n.* (H). Southwest Finland: Houtskär, 11 Aug. 1937, *Ole Eklund s.n.* (H). Uusimaa: Ab. Karjalohja, Karkali Nature Reserve, 3 Jul. 1989, *M. Kiirikki, A. Koponen & T. Koponen 44783* (H), 44787 (H), *44790* (H), 6 Jul. 1989, *44802* (H), *44806* (H), 10 Jul. 1989, *44810* (H), *44817* (H), *44823* (H), 12 Jul. 1989, *44835* (H), *44837* (H), *44846* (H).

France. Bourgogne-Franche-Comté: Chailluy, 29 Aug. 1940, *L. Hillier s.n.* (PC); Haute-Saône, 22 Dec. 1985, *Frahm & Millon s.n.* (H). Bretagne: La Roche Mausice, May 1894, *L. Bason 104-1* (NSW). Grand Est: Vosges, Gerbamont, 1860, *Pièrrat* (NSW), 10 Sep. 1881, *Pièrrat* (H), 22 Aug. 1883, *Pièrrat s.n.* (H); Rochesson, 28 Jul. 1867, *Pièrrat s.n.* (H), 22 Jul. 1881, *Pièrrat* (NSW); s. loc., Ranska, 1874, *illegible handwritten name* (H), 2 Aug. 1883, *Pièrrat s.n.* (H), 1867, *illegible handwritten name* (H). La Reunion: Plaine der Cafter, s. date, *Bernier s.n.* (PC). Normandie: Cherbourg, Jun. 1884, *illegible handwritten name* (H). Nouvelle-Aquitaine: Eaux Bonnes, *B. Sprucei s.n.-2* (H); Gan, *s.n.* (H); Jurançon, *s.n.* (H). Occitanie: Gasques, *B. Sprucei s.n.* (H); Hautes-Pyrénées, Sep. 1898, *s.coll.* (H). SAINT PIERRE AND MIQUELON: He Miquelon, *Dr. Delamare 98* (MICH).

Germany. BADEN-WÜRTTEMBERG: Baden, 17 Sep. 1858, *Jack s.n.* (MICH); Schwarzwälder, 21 Mar. 1862, *R. Lehr s.n.* (HBG), 14 Oct. 1862, *F. Elmendorff s.n.* (HBG). BAVARIA: Eichstätt, *Arnold s.n.* (H); Oberbayern, 27 Sep. 1947, *G. Schwenker s.n.* (HBG), Jun. 1947, *s.n.* (HBG), 15 Dec. 1918, *D. Schellenberg s.n.* (HBG); Partenkirchen, 1857, *Arnold s.n.* (H); Swabia, Harburg, *s.coll.* (HBG). HESSE: Wetterau, *illegible handwritten name* (H3150490, 3150549). LOWER SAXONY: Hannover, *Ehrhart s.n.* (H). NORTH RHINE-WESTPHALIA: Bielefeld, *H. Wagner s.n.* (H). RHINELAND-PALATINATE: Nahe area, *s.coll.* (MICH); illegible handwritten locality, Jun. 1925, *illegible handwritten name* (H); Sankt Goar, 24 Jul. 1874, *G. Herpell s.n.* (HBG). RHINE-WESTPHALIA: Waldbröl, 1 Oct. 1825, *illegible handwritten name* (H). SAXONY: Erzgebirge, Jul. 1934, *A. Kopsch 517* (MICH).

Hungary. COMIT. VAS.: 11 Jul. 1955, *L. Vajda s.n.* (H).

Ireland. CONNACHT: Lough Mask, 21 May 2003, *D. T. Holyoak s.n.* (BBSUK); Lough Ree, 5 Jul. 2002, *N. G. Hodgetts s.n.* (BBSUK). LEINSTER: Kildare Co., 1 Sep. 2005, *D. T. Holyoak 05-464* (BBSUK); Offaly Co., 15 Aug. 2005, *D. T. Holyoak 05-382* (BBSUK). MUNSTER: Cork Co., Gougane Barra, 11 Aug. 2002, *T. L. Blockeel s.n.* (BBSUK), Knocknagree, 16 Sep. 1955, *s.coll.* (BBSUK); Killarney, Jun. 1873, *L. O. Z. s.n.* (H). ULSTER: Monaghan Co., 5 Aug. 2005, *S. D. S. Bosanquet, C. D. Preston, R. D. Porley, S. J. Thomas & R. S. Weyl s.n.* (BBSUK).

Italy. Rasmaceto'an Buchen, 9 Oct. 1896, *M. Fleischer s.n.* (H).

Japan. AKITA: 7 Oct. 1977, *Y. Takahashi YT-3291-1* (AKPM), 13 May 1979, *YT-4084* (AKPM), 17 Jun. 1979, *YT-4255* (AKPM), 15 Jun. 1979, *YT-4271* (AKPM), 14 Jun. 1980, *YT-5199* (AKPM), 26 Aug. 1984, *YT-8006*; 26 May 1984, *YT-7572-1* (AKPM), 23 Jun. 1985, *YT-8295* (AKPM), 28 Jul. 1996, *YT-11110* (AKPM), *YT-11112* (AKPM), 21 May 2005, *YT-12608* (AKPM), 4 Nov. 2005, *YT-13179* (AKPM), 20 Nov. 2005, *YT-13225* (AKPM), *YT-13229* (AKPM), 14 May 2006, *YT-13332* (AKPM), *YT-13391* (AKPM), 24 Jun. 2006, *YT-13476* (AKPM). FUKUI: Rokuromi, 18 Jun. 1972, *A. Sakai 327* (TNS). FUKUSHIMA: Mt. Iide, 31 Jul. 1959, *Y. Watanabe 3872* (TNS). HIROSHIMA: s. loc., 34°41′ N, 132°11′ E, 27 Jun. 1987, *M. Higuchi s.n.* (H). HOKKAIDO: Kushiro, 21 Sep. 2003, *W. B. Shofield 122394* (UBC), *122395* (UBC), *122407* (UBC), *122415* (UBC), *122418* (UBC), *122423* (UBC). HYOGO: Haga, 13 Sep. 2003, *M. Hayashi 11117* (HYO), *K. Une 9342* (HYO), 14 Sep. 2003, *M. Hayashi 10994* (HYO), *A. Yoshiharu 10125* (HYO); Ichijima, 6 Mar. 2000, *H. Akiyama 14749* (HYO); Nankou, 28 Jun. 2003, *Y. Tateishi 16812* (HYO); Sayou, 9 Nov. 2003, *N. Naoki 11379* (HYO). ISHIKAWA: Kakuma, 12 Nov. 1995, *H. Akiyama 13197* (HYO). KAGOSHIMA: Mts. Kirishima National Park, 16 Dec. 1958, *Z. Iwatsuki s.n.* (MICH). KANAGAWA: Hatano, Mt. Jogadake, 29 Aug. 1961, *Y. Watanabe 7150* (TNS). KYOTO: Miyama, 2 May 1960, *T. Nakajima s.n.* (MICH); Yakuno, 6 Oct. 1967, *M. Mizutani s.n.* (HIRO, HYO, MICH, PC). MIE: Suzuka Mts., 23 Nov. 1951, *N. Takaki s.n.* (H, MICH). MIYAGI: Katta, Mt. Zao area, 7 Aug. 1956, *Y. Watanabe 1985* (TNS). NARA: Mt. Odaigahara, 16 Jun. 1963, *T. Nakajima s.n.* (MICH), 20 Aug. 1966, *s.n.* (MICH). NIIGATA: Nagaoka, 9 May 1948, *Y. Lkegami 9689* (MICH). OSAKA: Kaizuka, 29 Mar. 1949, *T. Nakazima 843(b)*, 10 Apr. 1960, *10307* (OSA). SAITAMA: Chichibu, 20 Aug. 1968, *Y. Watanabe 14431*

(TNS). Tochigi: Nikko, 36°46′ N, 139°24′ E, 9 Sep. 1999, *M. Higuchi s.n.-2* (MICH). Tokushima: Mima, Mt. Tsurugi, 11 Sep. 2001, *M. Higuchi s.n.* (BISH), *1117* (MICH). Yamaguchi: Atô, 15 Sep. 1977, *T. Shiomi 21037* (HIRO); Kitakoma, 5 Aug. 1961, *Y. Watanabe 6549-2* (TNS); Hara, 2 Oct. 2000, *H. Deguchi 35377* (HIRO); Nakakoma, 20 Aug. 1974, *Y. Watanabe 21388* (TNS).

Latvia. Courland: Kreis Talsen, 25 May 1909, *J. Mikutowicz 355* (H3150551, 3150521); Usma, 5 Jun. 1931, *s.coll.* (H). Vidzeme: Kreis Wolmar, Jul. 1910, *J. Mikutowicz s.n.* (H3150649, 3150650).

Netherlands. Gelderland: Wolfheze, *illegible handwritten name* (H), *L. H. Buse en Mevr. Buse geb. Koppiers 108* (H). North Brabant: Eindhoven, 14 Dec. 2003, *A. Juslén 1738a* (H).

New Zealand. Canterbury: Broad Stream, above Cora Lynn Station, 9 Mar. 1989, *A. J. Fife 9186* (CHR). Hawke's Bay: near Lake Waikaremoaua, 15 Jan. 1935, *G. O. K. Sainsbury s.n.* (S). Nelson: Scarlett Range, Shelter, 8 Feb. 1987, *A. J. Fife 8042* (MICH), 9 Feb. 1987, *8084* (MICH). Manawatu-Wanganui: Rangitikei Co., Northwest Ruahine, *J. K. Bartlett s.n.* (AM). Southland: Fiordland, Windward River, 19 Apr. 2002, *M. Renner s.n.* (CHR), 20 Apr. 2002, *T. Paul s.n.* (CHR). Taranaki: Dawson Falls Bush, Sep. 1946, *W. Martin s.n.* (CHR); Mt. Egmont, *G. O. K. Sainsbury 777* (BM *s.n.* as *U. pygmaeothecia*). Tasman: Golden Bay Co., Dec. 1978, *J. K. Bartlett s.n.* (AM). Waikato: base of Mount Ruapehu, 3 Dec. 1984, *H. P. Ramsay & J. Beever 98/84* (NSW).

Norway. Akershus: Söndre Hallangen, 5 Apr. 1960, *T. Ahti 12419* (H). Hordaland: Osterøy, 18 Aug. 1992, *J. Hernrichs 227* (H3230277, 3230280); Stord, Leiriik, 31 Aug. 1927, *M. J. Kotilainen s.n.-2* (H). Møre og Romsdal: Volda, Bjirkdalen, 31 Jul. 1920, *M. J. Kotilainen s.n.-1* (H). Nordland: Torghatten, 22 Aug. 1911, *s.coll.* (H). Rogaland: Egersúnd, Jul. 1889, *N. Bryhn s.n.-3* (NSW); Ryfylke, Jul. 1889, *s. n.* (NSW). Sør Trøndelag: Sör Tröndelag, 26 Apr. 1994, *S. Laaka 3730* (H); Trondhjem, Jul. 1884, *I. Hagen s.n.* (H), Jul. 1907, *N. Bryhn s.n.-2* (NSW). Telemark: Porsgrunn, Jun. 1865, *Cleve s.n.* (H).

Poland. Prešov Region: East Carpathians, 13 May 1973, *R. Ochyra s.n.* (MICH), Slonne Gory Hills, 13 May 1973, *R. Ochyra s.n.* (H). Tomaszów Lubelski Co.: Roztocze, 30 Mar. 1957, *S. Lisowski s.n.* (H), 1 May 1964, *K. Karczmarz s.n.* (H).

Portugal. Aveiro: Mealhada, 25 May 1972, *J. Suominen 1843* (H). Azores: Pico, 1937, *H. Persson s.n.* (H). Porto: s. loc., 1856, *G. L. Sjögren s.n.* (H).

Russia. Altai: Teletzkoye Lake, 51°45′ N, 87°35′ E, 24 Jun. 1991, *M. Ignatov s.n.* (H, MICH). Caucasus: s. loc., 3 Jul. 1877, *V. F. Brotherus s.n.* (H). Khabarovsky: Komsomol'skiy Distr., 10 Jun. 1986, *V. Y. Cherdantseva s.n.* (PE); Sovgavaskiy, 2 Aug. 1972, *V. Y. Cherdantseva s.n.* (PE); Ulchsky Distr., 51°29′ N, 140°4′ E, 6 Sep. 1976, *P. Alanko 31804* (H), 8 Sep. 1976, *32174* (H), *32176* (H). Sakhalin: Due, Aug. 1861, *Glehn s.n.* (H); s. loc., 46°54′15.4″ N, 143°03′0.5″ E, 29 Jul. 2001, *V. Y. Cherdantseva s.n.* (PE).

Slovakia. Prešov Region: Mts. Vsoké Tatry, Aug. 1947, *Z. Pilous s.n.* (H), Aug. 1948, *s.n.* (H). Žilina Region: Tatry Zachodnie, 20 Jul. 1912, *Z. A. Zmuda 119* (H).

Slovene. Carniola: Kokra, 20 Aug. 1881, *J. B. s.n.* (H).

Spain. Galicia: Pontevedra, *H. Buch s.n.* (H).

Sweden. Gotland: Fleringe, Jul. 1856, *P. T. Cleve s.n.* (H). Halland: Fröllinge, Aug. 1860, *S. O. Lindberg s.n.* (H). Närke: illegible handwritten locality, 9 Jun. 1884, *E. Adlerz s.n.* (H), 5 Oct. 1884, *s.n.* (H); Örebro, May 1870, *J. J. Johansson s.n.* (H); 14 Jul. 1862, *C. H. s.n.* (H). Skåne: Gyllebo, 4 Jun. 1938, *A. Hovgard s.n.* (H); s. loc., 7 Jul. 1875, *H. L. s.n.* (H), 19 Jul. 1937, *illegible handwritten name* (H); Skäralid, Aug. 1884, *H. Thedenius s.n.* (H); Sövestad, Jul. 1883, *A. Grönvall s.n.* (H); Tjörnarp, May 1893, *H. Möller s.n.* (MICH); Tydinge, Broby, 1872, *C. O. Hamnström s.n.* (H3150656), *s.n.* (H3150388). Småland: Åminne, 26 Jul. 1875, *C. A. Andersson s.n.* (MICH); Burseryd, Jun. 1877, *K. A. T. Seth. s.n.* (H); Hesselby Wada, 11 Aug. 1887, *R. Tolf s.n.* (H2056071, 2056072); s. loc., 15 Aug. 1870, *illegible handwritten name* (H). Södermanland: Sicklasjön, Jul. 1852, *S. O. Lindberg s.n.* (H); Utö, 24 Jul. 1965, *E. Nyholm* (S). Uppland: Hagaparken, Feb. 1859, *S. O. Lindberg s.n.* (H). Väster Götaland: Göteborg, Nov. 1913, *E. Hjertman s.n.* (H3150406, 3150568), Jan. 1915, *s.n.* (H); Halleberg, *illegible handwritten name* (H); Marstrand, 1889, *A. Arvén s.n.* (H); s. loc., Sep. 1932, *C. Sandberg s.n.* (H); Österplana, *S. O. Lindberg s.n.* (H). Västmanland: Viker, creek valley between Älvlången and Grytsjön, 18 Aug. 1966, *T. Koponen s.n.* (H).

Switzerland. Lake Geneva: Saint-Cergue, Jul. 1864, *Jack s.n.* (MICH). North East: canton of Glarus, 11 Nov. 1946, *H. T. Shacklette 2555* (MICH).

Turkey. Giresun: Bulancak to Kovanlik, *E. Nyholm 258a/82* (S).

U.K. England: Bridlington, 30 Aug. 2006, *C. Wall 118-3* (BBSUK); Castle Howard, *Spruce s.n.* (H3150391, 3150393, 3150394); Colwick Country Park, 25 Jun. 2006, *T. L. Blockeel 35/206* (BBSUK); Cumberland, Borrowdale, Oct. 1924, *C. H. Brinstead s.n.* (H); Flitwick, 10 Sep. 2006, *T. L. Blockeel 35/232* (BBSUK); Holmbridge, 8 Apr. 1884, *W. B. Waterfall 320-2* (NSW); Pleasley Vale, 16 Nov. 2002, *T. L. Blockeel s.n.* (BBSUK); Scout Scar, 4 Jun. 2006, *T. L. Blockeel 35/204* (BBSUK); Surrey, 1954, *A. W. E. Scudder 99/5* (UBC); Teesdale, 23 Sep. 1853, *W. Smith* (NSW); Thetford Warren, 8 Jan. 2001, *R. J. Fisk s.n.* (BBSUK); Thorpe Salvin, 25 Nov. 2000, *T. L. Blockeel 29/512* (BBSUK); Westmorland, Aug. 1855, *illegible handwritten name* (MICH); Yorkshire, Aug. 1838, *illegible handwritten name* (H). Northern Ireland: Ballycastle, 22 Jul. 1870, *illegible handwritten name* (H). Scotland: Arbroath, 24 Nov. 1883, *W. Smith s.n.* (H); Bernii Eigle Reserve, Jun. 1952, *H. A. Fairlet s.n.* (E); Clova-Angus, Jul. 1884, *W. Smith* (NSW); Cullaloe, 12 Jan. 2006, *D. F. Chamberlain & E. M. Kungu s.n.* (E213304, 213706); Isle of Skye, 16 Jun. 1962, *D. A. Ratcliffe s.n.-1* (E); Midlothian, 17 Sep. 2006, *D. F. Chamberlain s.n.* (E), Edinburgh, 26 Mar. 2002, *D. F. Chamberlain s.n.* (E); Mid Ebudes, 1998, *P. J. Chamberlain s.n.* (E); New Galloway, Feb. 1884, *J. Mc Andrew* (NSW), Aug. 1884, *s.n.* (NSW), Nov. 1984, *W. B. Waterfall 241-1* (NSW); s. loc., 1865, *G. E. Hunt s.n.* (H3150556), Jul. 1865, *s.n.* (H3150535, 3150555); Loch Garry, 11 Apr. 1971, *D. G. Long 1282-2* (E); Port Geiraha, 25 Jul. 2007, *R. J. Fisk s.n.* (BBSUK); Pressmennan Wood, 12 Nov. 1993, *D. G. Long s.n.* (E); Selkirk, 15 Apr. 1999, *D. G. Long & P. Lusby s.n.* (E); Skye, Ascrib Islands, 23 Jun. 2010, *D. G. Long 39389* (E); Sutherland, 12 Sep. 1973, *N. Hakelier s.n.* (H); Torridon, 8 Sep. 1944, *W. Ross s.n.* (E); Trossachs- Loch Katrine, 4 Jul. 1868, *G. E. Hunt s.n.* (H, MICH); West Lothian, 28 Apr. 1998, *D. G. Long 27682* (E). Wales: Caernarvonshire, Beddgelert, Oct. 1857, *illegible handwritten name* (MICH), Llanberis, 5 Sep. 1924, *W. Bellerby 49* (H), Oct. 1951, *D. A. R. s.n.* (E); Merionethshire, Sep. 1904, *J. Duncan s.n.* (E); Pembrokeshire, 26 Feb. 2007, *S. D. S. s.n.* (BBSUK).

U.S.A. ALASKA: Izembek Nat. Wildlife Reserve, 55°10′ N, 162°30′ W, 5 Aug. 1977, *W. B. Schofield 108950-3* (UBC); Juneau, 7 Aug. 1967, *F. J. Hermann 22125* (MICH); Kenai Peninsula, Homer, 59.40° N, 151.37° W, 6–7 Jul. 1995, *W. B. Schofield 103641-1* (UBC); Ketchikan, 27 Apr. 1948, *W. J. Eyerdam 5001*, 10 Aug. 1967, *F. J. Hermann 22226* (DUKE); Yakutat, 18 Jul. 1945, *L. D. Stair* 4909 (MICH), 19 Jul. 1945, *4875* (MICH). CONNECTICUT: Plainville, 8 Feb. 1880, *illegible handwritten name* (MICH). GEORGIA: Rabun, 1 Sep. 1996, *C. Zartman 2551* (DUKE); Wacon, 3 Sep. 1947, *W. C. Steere 10130* (MICH). HAWAII: Maui, 26 Aug. 1967, *W. J. Hoe 1763.0* (MICH), 28 Aug. 1967, *1803.0* (H), 23 Jun. 1976, *4181.0* (H, MICH), Sep. 1973, *B. Harrison s.n.* (MICH). KENTUCKY: Pike Co., 9 Jun. 1941, *H. T. Shacklette 321* (MICH). MAINE: Hancock Co., Mount Desert, 14 Sep. 1920, *W. R. Taylor 3310* (MICH), 3 miles SW of Brooksville, 25 Aug. 1962, *H. D. Hammond s.n.* (NSW); Knox Co., 26 Aug. 1987, *B. H. Allen 6081A* (MICH); Lincoln Co., 2 Sep. 1979, *B. Allen 1339* (MICH); York Co., 43°13′01″ N, 70°41′42″ W, May 2000, *R. A. Pursell 12112* (DUKE). MASSACHUSETTS: Berkshire Co., 30–31 May 1909, *S. H. Burnham s.n.* (MICH); Essex Co., Salem, 8 Aug. 1864, *Jack s.n.* (MICH). MICHIGAN: Alger Co., 28 Jul. 1940, *E. M. Wells 1363* (MICH), 27 Jul. 1978, *F. J. Hermann 28508* (MICH); Alpena Co., 8 Apr. 1855, *H. Robinson & A. J. Sharp s.n.* (MICH); Aun Aston, 19 Jul. 1930, *W. C. Steere s.n.* (MICH); Charlevoix Co., 24 Jul. 1969, *H. Crum s.n.* (H, MICH); Cheboygan Co., 15 Aug. 1981, *R. & I. Duell 1030./2a* (MICH), Burt Lake, Jun-Aug. 1920, *G. E. Nichols 313* (MICH), 2 Aug. 1940, *H. A. Gleason, Jr. 2960* (MICH), Carp Creek, 11 Jul. 1936, *F. M. Pagan s.n.* (MICH), 12 Aug. 1938, *D. B. O'Brien s.n.* (MICH), Douglas Lake, 14 Jul. 1928, *F. J. Hermann s.n.* (MICH); Chippewa Co., 5 Jul. 1968, *D. H. Vitt 838* (MICH), *841* (MICH), 10 Sep. 1929, *J. L. Thorpe s.n.* (MICH), Sugar Island, Jun. 1933, *W. C. Steere 3201* (MICH), *3324-1* (MICH), *3493* (H, MICH), Vermilion, 3 Jul. 1914, *A. H. Povah Shiras 68* (MICH), *A. H. W. Povah s.n.* (MICH); Clinton Co., 13 Jul. 1944, *P. L. D. Stair 4519* (MICH); Grand Traverse Co., near Mayfield, 20 Aug. 1931, *W. C. Steere 356* (MICH); Gratiot Co., 3 Apr. 1938, *I. Schnooberger 787* (MICH), Alma, 28 Mar. 1893, *C. A. Daris s.n.* (MICH); Holland, 9 Aug. 1910, *C. H. Kauffman s.n.* (MICH513256, 513263); Huron Co., 9 Oct. 1938, *I. Schnooberger 1817* (MICH); Keweenaw Co., 6 Mar. 1977, *S. Trynoski s.n.* (MICH), 1 Oct. 1978, *F. J. Hermann 28731* (MICH), Smithwich Island, 1 Jul. 1930, *A. H. Povah 37* (MICH); Lake Michigan, 25 Sep. 1978, *F. J. Hermann 28631* (MICH); Mackinac Co., Mackinac Island, 16–18 Aug. 1921, *G. E. Nichols 167* (MICH), 27 Jul. 1935, *H. A. Gleason Jr. s.n.* (MICH), 9 Aug. 1968, *H. Crum s.n.* (H, MICH), 10 Aug. 1968, *D. H. Vitt 1163d* (MICH); Marquette Co., 20 Jun. 1971, *F. J. Hermann 23772* (MICH); Mecosta Co., Croton, 10 Oct. 1937, *I. Schnooberger 218* (MICH); Montclam Co., 27 Mar. 1938, *I. Schnooberger 753* (MICH); Oakland Co., Sep. 1977, *A. Fife s.n.* (MICH); Ontonagon Co., Porcupine Mts., 20–27 Aug. 1935, *G. E. Nichols & W. C. Steere s.n.* (MICH). NEW HAMPSHIRE: Carroll Co., 19–24 Apr. 1908, *H. H. Bartlett 1241* (MICH); Lebanon, May 1995, *G. G. Kennedy 774-1* (MICH); Monadnock Mt., 25 Aug. 1956, *H. Crum & L. Anderson 7919* (MICH); Marlow, Sand Pond, 8 Feb. 1938, *W. S. Allen & L. D. Stair 281* (MICH), 3 Aug. 1939, *s.n.*

(MICH). New Jersey: Morris Co., 31 Mar. 1918, *W. R. Taylor 2645* (MICH). New York: Adirondack Mts., 13 Aug. 1934, *A. H. Smith s.n.* (MICH), 23 Aug. 1934, *G. D. Darker 5102* (MICH), 18 Aug. 1957, *F. J. Hermann 13816* (MICH), 20 Aug. 1957, *13880* (MICH); Adirondack Reserve, 25 Sep. 1898, *E. G. Britton s.n.* (MICH); Buffalo, *G. W. Clinton s.n.* (MICH537890, 537914); Catskill Mts., Aug. 1868, *Cleve s.n.* (H2048059, 2056087); Clinton Co., 13 Jul. 1973, *S. J. Smith 49885* (MICH); Delaware Co., 13 Apr. 1952, *K. L. Brooks 1126* (MICH); Essex Co., 8 May 1936, *G. D. Darker 6682* (MICH), 30 Aug. 1950, *E. H. Ketchledge 791* (MICH), 30 May 1959, *T. C. Baim 4805* (MICH), 3 Sep. 1965, *S. J. Smith 38724* (MICH), 25 Aug. 1963, *P. L. Redfearn, Jr. s.n.* (MICH); Hamilton Co., 8 Sep. 1950, *E. H. Ketchledge 842* (MICH), 28 Jul. 1961, F. J. Hermann 16897 (MICH), 13 May 1968, *S. J. Smith 42472* (H); Lake George, 13 Nov. 1914, *s.coll.* (MICH); Lake Placid, 9 Sep. 1898, *E. G. Britton s.n.* (MICH); Rensselaer Co., 5 Dec. 1959, *S. J. Smith 29854* (MICH); Saranac Lake, Hoel Pond, 26 Aug. 1914, *E. B. Mains s.n.* (MICH); Saratoga Co., 30 Apr. 1955, *S. J. Smith 18131* (MICH); Suffolk Co., 26 Feb. 1957, *R. Latham 34407* (MICH); Tompkins Co., Ithaca, 4 Jul. 1903, *C. H. Kauffman s.n.* (MICH); Warren Co., 21 May 1966, *S. J. Smith 40003* (MICH). North Carolina: Alexander Co., 20 Sep. 1968, *D. H. Vitt 1343* (MICH); Avery Co., 1 Apr. 1978, *J. Rohrer 454* (MICH), Grandfather Mt., Jul. 1891, *J. K. Small s.n.* (MICH); Buncombe Co., Craggy Gardens, 16 Jul. 1958, *W. B. Schofield 9254* (MICH); Jackson Co., 20 Sep. 1968, *D. H. Vitt 1345-2* (MICH), *1346-2* (MICH), *1348* (MICH), *1349* (MICH), *1350-2* (MICH), 21 Sep. 1968, *1360-2* (MICH); Macon Co., 3 Sep. 1957, *L. E. Anderson 12918* (H), Highlands, 2 Sep. 1947, *W. C. Steere 10010* (MICH), 22 Sep. 1968, *D. H. Vitt 1365* (MICH), *1368* (MICH), *1369* (MICH), Franklin, 14 Jun. 1964, *F. J. Hermann 19402* (MICH); illegible handwritten locality, 3 Sep. 1947, *W. C. Steere 10231a* (MICH); Roan Mt., Feb. 1897, *A. G. Wetherby s.n.* (H, MICH), 15 Jun. 1936, *W. H. Welch 2881* (MICH); Swain Co., 7 Jul. 1935, *L. E. Anderson 3296* (MICH), 23 Sep. 1968, *D. H. Vitt 1380-2* (MICH), *1381* (MICH); Transylvania Co., 21 Sep. 1968, *D. H. Vitt 1399* (MICH); Watauga Co., 30 Jun. 1978, *J. Rohrer 606* (MICH); Yancey Co., 35°45′ N, 82°16′ W, 28 Jun. 1978, *D. H. Vitt & D. G. Horton s.n.* (H, MICH). Ohio: Hamilton Co., 7 Sep. 1967, *S. J. Smith 42096* (MICH); Hocking Co., 1 Sep. 1968, *H. Crum s.n.* (MICH). Oregon: Coos Co., 43°19′ N, 124° 22′ W, 12 Aug. 2000, *M. J. Price 1875* (MO); Lincoln Co., 44°18′ N, 124°06′ W, 17 Jun. 1992, *D. H. Norris 78451* (H); Mulnomah Co., *F. Mackaness s.n.* (MICH). Pennsylvania: Clinton Co., 13 Jul. 1944, *L. D. Stair 4520* (MICH), *4522* (MICH), *4524* (MICH); Lancaster and Lebanon county line between Mt. Hope and Penryn, 8 Apr. 1892, *J. K. Small s.n.* (MICH). South Carolina: Pickens Co., 31 Aug. 1957, *L. E. Anderson 12885* (MICH). Tennessee: Blount Co., 5 Mar. 1953, *A. J. Sharp 534* (MICH); Cocke Co., *C. T. Bryson 2938d* (MICH); Polk Co., Big Frog Mt., 19 Mar. 1939, *A. J. Sharp 3954* (MICH); Seiver Co., Mount Le Conte, 5 Sep. 1947, *W. C. Steere 10494* (MICH), 6 Sep. 1947, *10615* (MICH), 12 Jul. 1959, *W. B. Schofield 10357* (H, MICH), 10 May 1978, *C. T. Bryson 1991* (MICH), 15 May 1986, *2993* (MICH), *3006* (MICH). Vermont: Essex Co., 44°34′ N, 71°50′ W, 16 May 2008, *J. Shaw 15435* (DUKE), 44.99620°N, 71.69815°W, 19 May 2008, *B. Shaw 7134* (DUKE), *7135* (DUKE); Newfane, 30 Jun. 1934, *A. J. Grout s.n.* (MICH), *251* (MICH). Virginia: along Fox Creek, 16 Jun. 1892, *A. M. Vail & E. G. Britton s.n.*

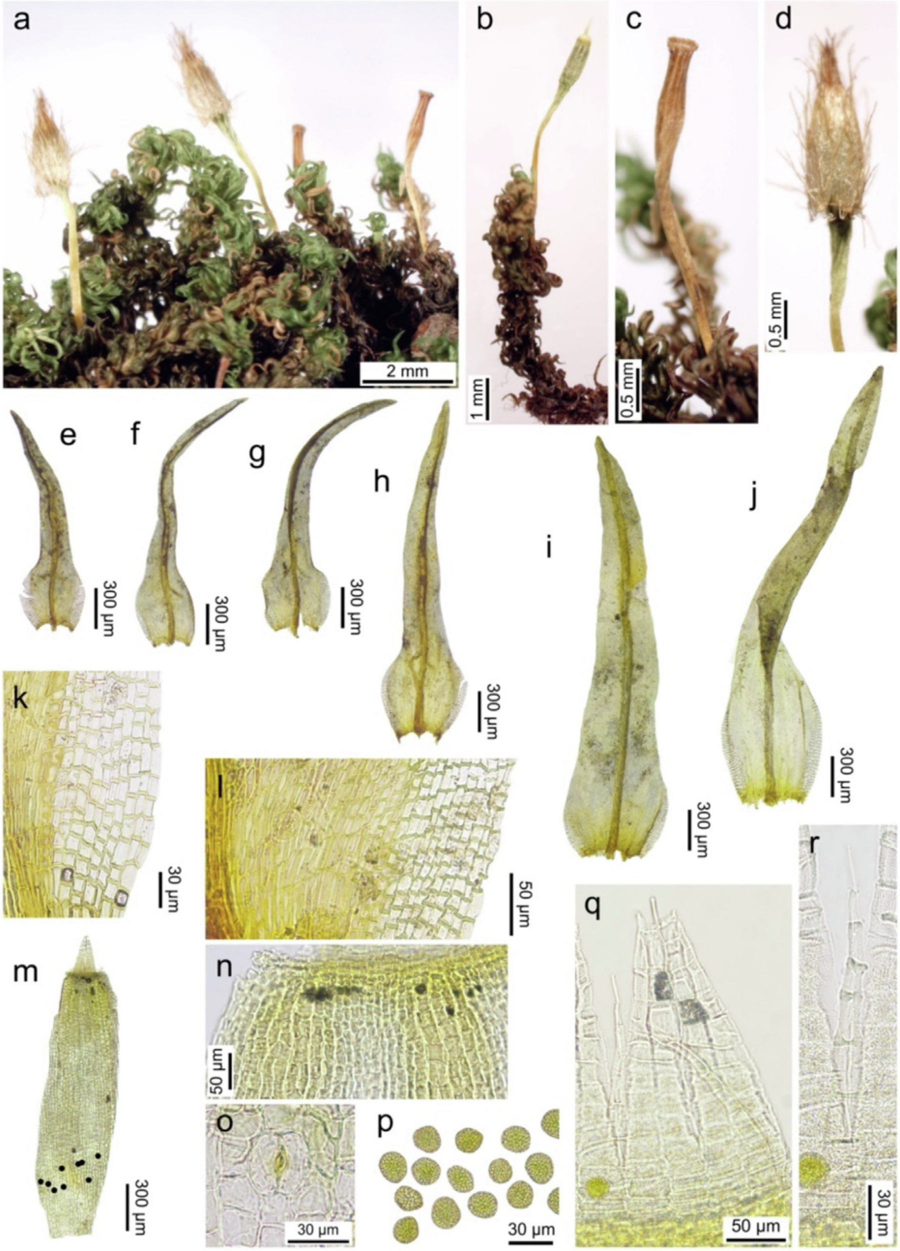


Fig. 44 – *Ulota crispa* (Hedw.) Brid from China. a–b. Habit. c. A capsule in dry and empty. d. Calyptra. e–h. Leaves. i–j. Perichaetial leaves. k–l. Marginal cells at leaf base. m. Exothecial wall, with dots indicating stoma position. n. Exothecial cells near the mouth. o. Stoma. p. Spores. q. Peristome. r. Endostome segment. (All from *S.-J. Li 116* [non-type, PE]).

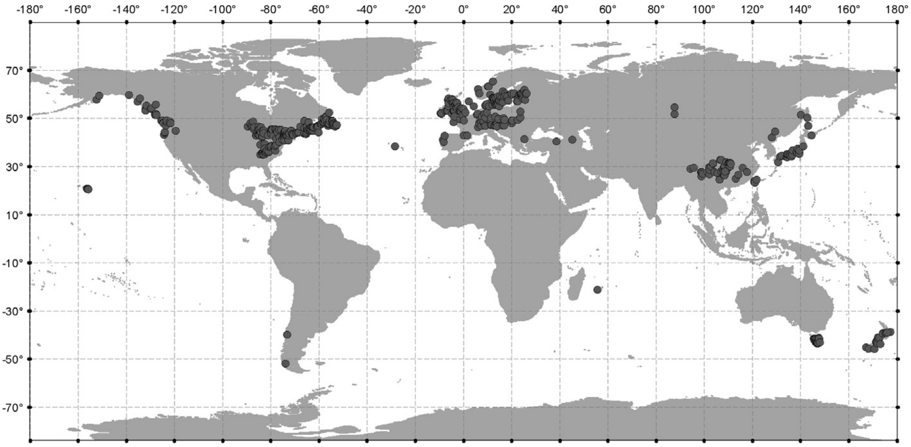


FIG. 45 – Distribution of *Ulota crispa* worldwide.

(MICH); Cheat Bridge, 15 Aug. 1906, *J. L. Sheldon 2545* (MICH); Grayson Co., 3 May 1969, *D. H. Vitt 1448* (MICH), *1453* (MICH); Greene Co., Shenandoah National Park, 22 Jun. 1944, *I. Schnooberger & F. E. Wynne 3285* (MICH), 23 Jun. 1944, *3334* (MICH); Madison Co., Shenandoah National Park, Blue Ridge Mts., 19 May 1966, *F. J. Hermann 20382* (H, MICH); Nicholas Co., 18 Apr. 1998, *J. B. Nelson 19061* (DUKE); Page Co., Shenandoah National Park, Hawksbill Mt., 16 Jun. 1944, *I. Schnooberger & F. E. Wynne 3069* (MICH), *I. Schnooberger 4853* (MICH); Preston Co., 6 Jul. 1946, *N. Ammons 15* (MICH); Pocahontas Co., 14 May 2000, *J. Shaw 10359* (DUKE), Durbin, 22 Sep. 1904, *J. L. Sheldon 1060* (MICH), *2266* (MICH); Randolph Co., 15 Aug. 1906, *J. L. Sheldon 2545* (MICH), Spruce Knob, 20 May 1978, *T. E. Weaks s.n.* (MICH); Rappahannock Co., Shenandoah National Park, Little Devils Stairs, 20 Jun. 1944, *I. Schnooberger & F. E. Wynne 3264* (MICH); Washington Co., Whitetop Mt., Blue Ridge, 11–12 Aug. 1892, *J. K. Small s.n.* (MICH), 28 May 1892, *A. M. Vail & E. G. Britton s.n.* (MICH). WASHINGTON: Clallam Co., Cape Flattery, 9 Apr. 1935, *A. H. Smith 1881* (MICH), Ozette Lake, 1 Aug. 1950, *B. I. Brown & W. C. Muenscher 115* (MICH); Grays Harbour Co., 5 Jun. 1972, *M. G. Manuel 1488* (H); Snohomish Co., 12 Jul. 1966, *E. Lawton s.n.* (MICH), *5638* (H); Whatcom Co., 25 Mar. 1963, *R. R. Ireland, Jr. 7500* (H). WISCONSIN: Menominee Co., 6 Oct. 1978, *F. J. Hermann 28762* (MICH).

9. **ULOTA CRISPULA** Bruch ex Brid., Bryol. Univ. 1: 793. 1827. ≡ *Orthotrichum crispulum* (Bruch ex Brid.) Hornsch. ex B.S.G., Bryol. Eur. 3: 23. (fasc. 2/3). 1837. ≡ *Ulota crispa* var. *crispula* (Bruch ex Brid.) Hammar, Monographia ~Orthotrichorum~ et ~Ulotarum~ Sueciae 24. 1852. ≡ *Orthotrichum crispum* subsp. *crispulum* (Bruch ex Brid.) Nyl. & Sael., Herb. Mus. Fenn.: 66. 1859. ≡ *Weissia crispula* (Bruch ex Brid.) Lindb., Acta Soc. Sc. Fenn. 10: 12. 1871. *nom. illegitimate.* ≡ *Orthotrichum ulophyllum* subsp. *crispulum* (Bruch ex Brid.) Kindb., Bih. Svensk. Vet. Ak. Handl. 7 (9): 121. 1883. ≡

Weissia ulophylla var. *crispula* (Bruch ex Brid.) Braithw., Brit. Moss Fl. 2: 94. 1889. ≡ *Orthotrichum cupulatum* var. *crispulum* (Bruch ex Brid.) Torre, Zeitsch. Ferdinand 3, 35: 241. 1891. *nom. inval. in synon.* ≡ *Ulota crispa* subsp. *crispula* (Bruch ex Brid.) Hérib., Mémoires de l'Académie des Sciences, Belle-Lettres et Arts de Clermont-Ferrand 14: 333. 1899. ≡ *Ulota ulophylla* var. *crispula* (Bruch) Weim., Förteckning över Skandinaviens Växter. 2. Mossor (Andra Upplagan): 40. 1937. ≡ *Ulota ulophylla* subsp. *crispula* (Bruch) Giacom., Istituto Botanico della R. Università R. Laboratorio Crittogamico Pavia, Atti 4: 249. 1947. ≡ *Ulotrichum crispulum* (Bruch ex Brid.) B.S.G., Bryol. Eur. 3: 1. 1851. (fasc. 46–47. Consp. Vol. 3. I.). *nom. illegitimate.* TYPE: In arboribus sylvaticis c. Bipontium clar. Bruch detexit; a quo ut et a Funckio amice communicatum habemus. GERMANY. Rheinland-Pfalz, Zweibrücken. "An Waldbäumen bey Zweybrücken, *Bruch s.n.*" (lectotype, B31025201! designated by Caparrós *et al.*, 2016).

Plants 1–2.5 cm tall, yellowish green to green above, brown to black below. Stems usually branched. Leaves flexuous, slightly to moderately crisped when dry, patent to wide-spreading when moist, (2.1–) 2.3–2.4 mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex acuminate; leaf margin plane or irregularly partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (8–) 9–10 (–12) × 8–9 (–10) μm, thick-walled, with low papillae; basal inner cells rectangular to elongate-rectangular, (18–) 26–33 (–42) × (3–) 4–5 (–6) μm, with strongly thickened walls, smooth; basal marginal cells distinctly differentiated in (3–) 4–9 (–16) rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves are somewhat longer, (1.7–) 2.5–3.2 (–3.3) mm. Vaginula is naked or hairy. Seta (1.5–) 2–3.8 (–5.3) mm long. Capsule long exserted, 1.7–2 mm long. Urn cylindrical to short-cylindrical when dry and empty, slightly, sometimes moderately constricted below the mouth when dry, eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the transition zone between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, often lying on the exothecium, lanceolate, densely papillose on the outside, striate-papillose to papillose above, and striate to striate-papillose below on the inside, often with a hyaline halo at edges. Endostome segments 8, linear, often fragile, almost as tall as teeth, uniseriate, 1/4–1/6 width of teeth in the middle, hyaline, smooth outside, almost smooth or slightly scabrous inside. Opercula with a beak, short to moderately long. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (19–) 27–38 (–47) μm in diameter.

Illustration: figures 46–48.

Habitat: It grows on trunks of trees, but no phorophyte was recorded. Altitude ranges: 427–1453 m.

Distribution: It sporadically occurs in North Hemisphere, including Austria, China, Denmark, Finland, Japan, Norway, Sweden, and U.S.A. Figure 49.

Notes: *Ulota crispula* has been considered a variety or synonym of *U. crispa* for a long time until recently. Caparrós *et al.* (2016) used molecular data and a complete morphological comparison to reassess a complex of *Ulota crispa* and finally reinstated the species rank of *U. crispula* and *U. intermedia*. Their work has been followed by some authors later (Fedosov and Ignatova, 2018; Blockeel, 2017). However, we found that the key they provided is not easy to use in practice, as stated by Fedosov and Ignatova (2018). It is still far from clear to exactly distinguish the species in *Ulota crispa* complex worldwide. Nevertheless, considering the great variation in *Ulota crispa*, we temporarily accept their treatment here.

Caparrós *et al.* (2016) stated that *Ulota crispula* differs from *U. crispa* in the slightly or moderately crisped leaves, fewer rows (4–9) of hyaline cells at leaf basal margins, capsules that not or weakly constructed when dry and empty, urns tending to be short-cylindrical in shape and linear, slender endostome segments with thin cross-walls on the inside surface. They also suggested that *Ulota crispula* has exothecial bands formed by evenly pale yellow cells, visibly separated from the mouth by a ring of small thin-walled cells, and paired exostome teeth easily split after being recurved. However, these two characters often vary irregularly in our study (figures 44, 46 and 47).

Besides *Ulota crispa*, *U. crispula* is similar to *U. intermedia*, but the latter is distinguished by the leaves strongly crisped when dry, endostome segments linear to linear-lanceolate, not fragile, often with distinctly thickened and prominent cross-walls on the inside surface.

Key to *Ulota crispula* and its closely related species.

1. Capsules moderately to strongly constricted below the mouth when dry and empty; exostome teeth often bordered by a hyaline halo..................... *U. crispa*
1. Capsules often hardly or slightly constricted below the mouth when dry and empty; exostome teeth never bordered by a hyaline halo...............................2
2. Leaves strongly crisped when dry; endostome segments linear to linear-lanceolate, not fragile, often with distinctly thickened and prominent cross-walls on the inside.. *U. intermedia*
2. Leaves flexuous, slightly to moderately crisped when dry; endostome segments linear, slender and fragile, often with thin cross-walls on the inside... *U. crispula*

Additional specimens examined: **China**. SICHUAN: Aba Co., 10 Aug. 2007, *Y. Jia 09720* (PE); Daofu Co., 25 Jul. 2007, *Y. Jia 09409* (PE), *09412* (PE); Kangding Co., 27 Aug. 1997, *Y. Jia 02458* (PE), 10 Apr. 2021, *M.-Z. Wang 202104-1725* (PE); Luding Co., Hailuogou National Glacier Forest Park, 14 Apr. 2021, *Q.-H. Wang 2576* (PE), *2585-2* (PE); Shimian Co., Gongga Mountain Nature Reserve, Q.-H. Wang *2250* (PE), *2252* (PE), *2262* (PE), *2293* (PE); Yanyuan Co., 26 Jul. 1983, *M.-Z. Wang 22330* (PE).

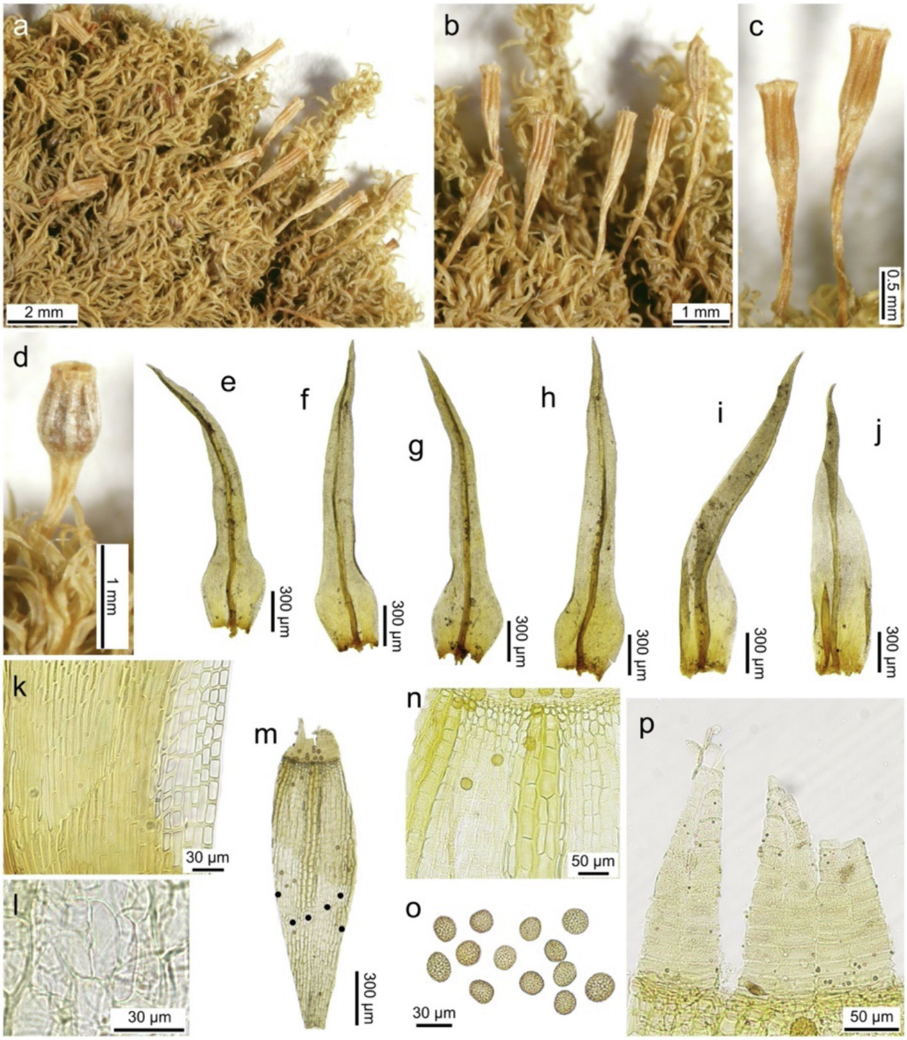


FIG. 46 – *Ulota crispula* Bruch. a–b. Habit. c–d. Capsules in dry, empty or not. e–h. Leaves. i. Outer perichaetial leaves. j. Inner perichaetial leaves. k. Marginal cells at leaf base. l. Stoma. m. Exothecial wall, with dots indicating stoma position. n. Exothecial cells near the mouth. o. Spores. p. Peristome, with endostome segments caducous. (All from the lectotype in B).

Denmark. JUTLAND: Ribe, 1 Jan. 1885, *O. Gelert s.n.* (H).

Finland. ÅLAND: Langbergsöde, 21 Sep. 1874, *J. O. Bomansson s.n.* (H).

Germany. BAVARIA: Allgäu, Oberstdorf, 2 Jul. 1949, *G. Schwenker s.n.* (HBG).

Japan. HOKKAIDO: Kamikawa, Ishikari River, 21 Aug. 1959, *S. Nakanishi 12343-2* (HYO). KAGOSHIMA: Yakushima Isl., Kamiyaku, 29 Jul. 2005, *H. Yokoyama 10147* (HIRO); MIYAZAKI: Nichinan, 4 Dec. 1963, *Z. Iwatsuki 251* (MICH), 19 Apr. 1958, *S. Hattori 35702* (S); NAGASAKI: Mt. Unzen, Jul. 1913, *T. Hirotie s.n.* (H).

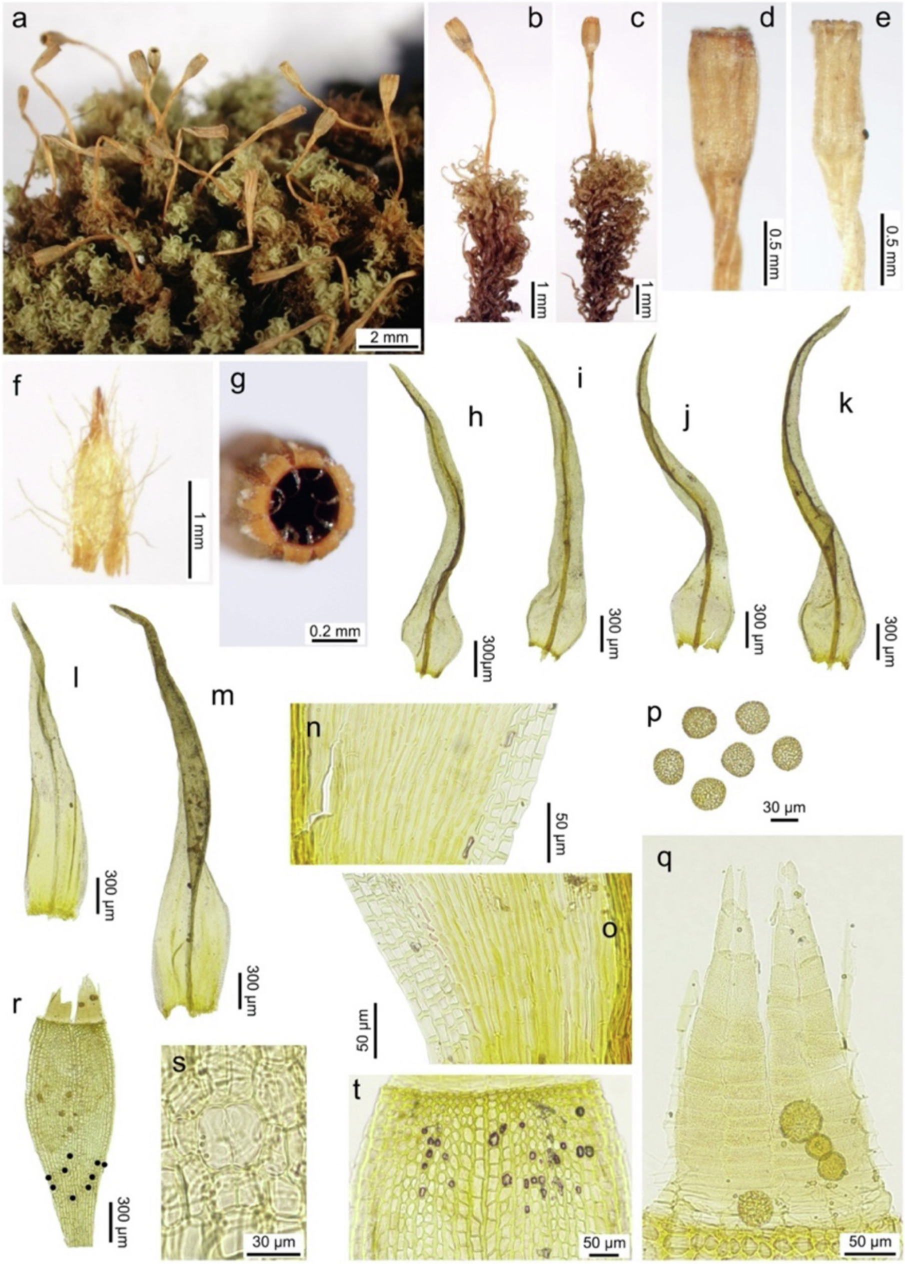


FIG. 47 – *Ulota crispula* Bruch from China. a–c. Habit. d–e. Capsules in dry and empty. f. Calyptra. g. Capsule mouth viewed from above. h–k. Leaves. l. Inner perichaetial leaf. m. Outer perichaetial leaf. n–o. Marginal cells at leaf base. p. Spores. q. Peristome. r. Exothecial wall, with dots indicating stoma position. s. Stoma. t. Exothecial cells near the mouth. (All from *Y. Jia 9720* [non-type, PE]).

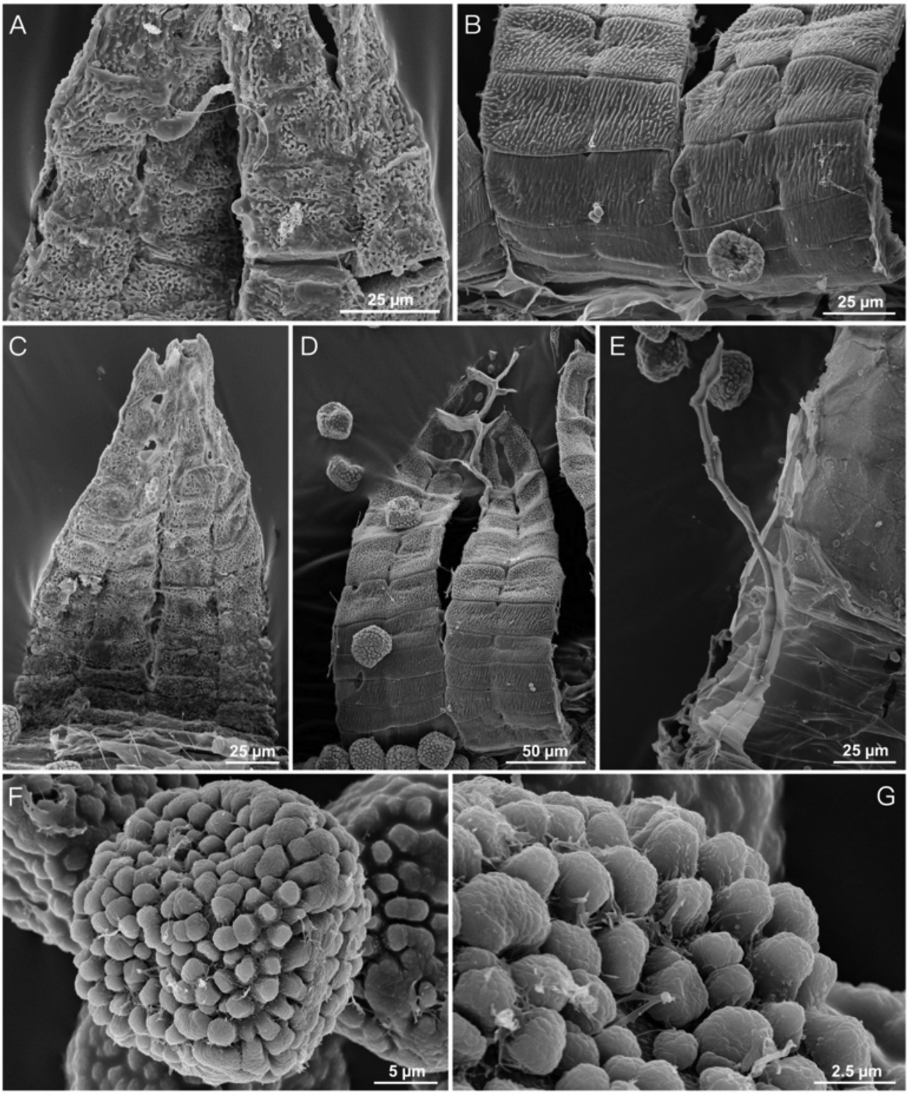


FIG. 48 – *Ulota crispula* Bruch. A, outer surface of exostome; B, inner surface of basal exostome; C, outer surface of exostome; D, inner surface of exostome; E, outer surface of endostome; F, spores; G, surface ornamentation of a spore. (All from *Jia 09409* [non-type, PE]).

Norway. SOGN OG FJORDANE: Solvorn par., 9 Sep. 2000, *Nils Lundqvist 21326* (S).

Sweden. SKÅNE: Tjörnarp, Aug. 1880, *Hartman 35* (H).

U.S.A. MAINE: Franklin Co., 70°43′51″ W, 45°09′30″ N, *R. A. Pursell 12857A-2* (MO). OREGON: Lincoln Co., 45°10′ N, 123°40′ W, 29 Mar. 1989, *W. B. Schofield 92892* (UBC). VERMONT: Essex Co., 44°34′ N, 71°50′ W, 16 May 2008, *J. Shaw 15435* (DUKE).

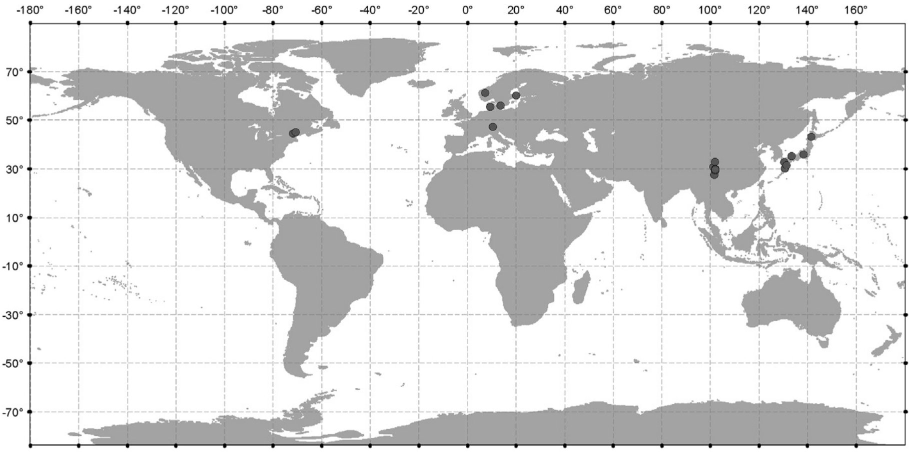


Fig. 49 – Distribution of *Ulota crispula* worldwide.

10. **Ulota curvifolia** (Wahlenb.) Lilj., Utkast Sv. Fl. (ed. 3): 546. 1816. ≡ *Orthotrichum curvifolium* Wahlenb., Fl. Lapp. 365. 1812. ≡ *Orthotrichum crispum* var. *curvifolium* (Wahlenb.) Wahlenb., Flora Suecica 2: 735. 1826. ≡ *Ulotrichum curvifolium* (Wahlenb.) Schimp., Bryologia Europaea 3: 1 (fasc. 46–47 Consp. vol. 3: I). 1851. *invalid, genus invalid.* ≡ *Weissia curvifolia* (Wahlenb.) Lindb., Journal of Botany, British and Foreign 11: 200. 1873. Type: Norway. "in saxorum lateribus umbrosis subirrigatis per partem sylvaticam Lapponiarum et inferalpinam Nordlandiae rarius", 17 Aug. 1807, *s.coll.* (holotype, S-B120865!).

Orthotrichum cirratum Bernh. ex Web. & Mohr, Bot. Taschenb. 237. 1807. *nom. nud. in synon.* Type: Germany. Erfurt.

Orthotrichum crispum var. *macrocarpon* Wallr., Flora Cryptogamica Germaniae 1: 211. 1831. *nom. illeg.* Type: Germany. ad arborum Thuringiae et Hercyn.

Orthotrichum laureri Hornsch., Flora 10: 656. 1827. *invalid, no description.* Type: Austria. Carinthiae super, in alpe Zircknitz supra Döllach.

Orthotrichum nicholsonii (Culm.) Culm., Musci Europaei et Americani Exsiccati 39: n. 1922. 1927. ≡ *Ulota nicholsonii* Culm., Revue Bryologique 53: 21. 1926. Type: Ireland. West Mayo, Achill Island, *Croaghaum, Rocks*, 20 Jul. 1925, *I. B. Duncan, H. H. Knight and W. E. Nicholson* (type, NY).

Orthotrichum scabridum (Kindb.) Kindb., European and N. American Bryineae (Mosses) 2: 306. 1897. ≡ *Ulota scabrida* Kindb., Catalogue of Canadian Plants, Part VI, Musci 83. 1892. Type: Canada. British Columbia, Rocky Mountains, abundant on immense boulders between Cathedral Mountain and Mount Stephen three miles below Hector, 29 Jul. 1885, *J. Macoun* (syntypes, PC! S!); also in the same place and on boulders by the torrent at Hector, Aug. 1890, *J. Macoun* (syntypes, CANM! MO1950025! PC0099343! S181367!).

Orthotrichum strictum Brid., Bryologia Universa 1: 289. 1826.

Ulota americana Mitten, Journal of the Proceedings of the Linnean Society 8: 26. 1864. Type: British N. America upon the rocks called Hell's Gates, *Drummond 153* (holotype, NY).

Ulota cirrata Grout, North American Flora 15A: 28. 1946. *illegitimate*

Ulota crispa var. *microcarpa* Brockm., Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg 23: 86. 1870. Type: Germany. Im Rabsteinfelder Holze bei Schwerin an Eichen (not located).

Ulota crispa var. *minus* (Schwägr.) Brid., Bryol. Univ. 1: 301. 1826. ≡ *Orthotrichum crispum* var. *minus* Schwägr., Species Muscorum Frondosorum, Supplementum Primum 2: 23. 1816.

Plants 2–3 (–4) cm tall, yellow to green above, dark brown to black below. Stems usually branched. Leaves variably stiffly flexuose, rarely crisped, when dry, erect-spreading to patent when moist, (1.4–) 1.6–2.2 (–2.4) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex acuminate; leaf margin plane or irregularly partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells round to oblong, (6–) 9–13 (–16) × (5–) 7–9 (–12) μm, thick-walled, with distinctly high, sometimes low papillae, often branched; basal inner cells linear, rectangular to elongate-rectangular, (21–) 27–40 (–55) × (1–) 2–5 μm, with strongly thickened wall, smooth; basal marginal cells weakly differentiated, 1–4, rarely 5 rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves somewhat longer, (1.5–) 1.7–2.2 (–2.3) mm. Vaginula naked to sparsely hairy. Seta 2–3.8 (–4) mm long. Capsule short to long exserted, (1.2–) 1.4–1.7 mm long. Urn subglobose when mature, short cylindrical when empty, slightly to moderately constricted below the mouth when dry, eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the transition zone between urn and neck. Preperistome rarely seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, often lying on the exothecium, lanceolate, strongly striate above, finely papillose below. Endostome segments 8, linear-lanceolate, almost as tall as teeth, uniseriate, 1/2–1/4 width of teeth in the middle, hyaline, smooth outside, almost smooth or slightly scabrous inside. Opercula with a beak, short to moderately long. Calyptra mitrate, moderately to strongly hairy, rarely sparsely hairy. Spores spherical, finely papillose, (16–) 19–24 (–28) μm in diameter.

Illustration: Nyholm (1960), Crum and Anderson (1981), Ignatov and Ochyra (1994), Wang and Jia (2012a) and Vitt (2014); figures 50–52.

Habitat: It grows on rocks, rarely on trees, such as alder. There are many records of altitude: (100–) 605–1500 (–2050) m. It is occasionally mixed with *U. hutchinsiae*.

Distribution: It is only common in boreal zone worldwide. Figure 53.

Notes: *Ulota curvifolia* is a distinct species and has the longest history in the genus. Its main diagnostic characteristics are flexuose, rarely crisped leaves with prominent conic or forked papillae cells, weakly differentiated leaf basal marginal cells, and strongly striolate exostome teeth. *Ulota curvifolia* is a mainly rock-growing moss, there are only two such cases in *Ulota* so far, and the other is *U. hutchinsiae*. Both have non-crisped leaves and weakly differentiated leaf basal marginal cells, but *Ulota hutchinsiae* differs in erect-appressed leaves, short leaf laminal papillae, cylindrical capsules (*vs.* short cylindrical), densely papillose exostome teeth, and smaller spores (13–14 μm).

Recently, a new record of *Ulota curvifolia* from Japan was reported (Suzuki and Iwatsuki, 2013). But it may be an error identification because in the Japanese population (*T. Suzuki 60547*, NICH) the leaves somewhat crisped and the exostome teeth densely papillose throughout, which is obviously inconsistent with the typical characteristics of this species, that is the erect to flexuose leaves and strongly striolate exostome teeth. Moreover, the length of the seta and capsules of the Japanese population is also quite different from ours.

No noteworthy variation was observed in *Ulota curvifolia*.

Key to *Ulota curvifolia* and its closely related species.

1. Leaves erect-appressed when dry; middle and upper leaf cells with short papillae; exostome teeth densely papillose; spores smaller, 13–14 μm; capsules cylindrical when dry.. *U. hutchinsiae*
1. Leaves erect to stiffly flexuose when dry; middle and upper leaf cells with prominent conic or forked papillae; exostome teeth strongly striate; spores relatively large, 19–24 μm; capsules short-cylindrical when dry............ *U. curvifolia*

Additional specimens examined: **Canada**. Alberta: Jasper National Park, 18 Jul. 1955, *H. Crum & W. B. Schofield 5093* (H, MICH); Lake Louise Alta, 13 Sep. 1904, *J. Macoun s.n.* (MICH536921, 536922). British Columbia: above Fort St. John, 30 Jun. 1943, *D. S. Correll 11878* (MICH), *11939* (MICH); head of Summit Lake above Fort Nelson, 124°40′ W, 58°38′ N, 18 Jul. 1943, *D. S. Correll 12005* (MICH); s. loc., 10 Jun. 1910, *Brinkman 217* (DUKE); Trail from Wapta Lake, Hector, to Lake O'Hara and Crystal Cave, 10 Jul. 1955, *H. Crum & W. B. Schofield 4503* (MICH); Wells Gray Provincial Park, 1 Jul. 1961, *Leena & T. Ahti 7314* (H, MICH), *13693* (H). Labrador: Churchill Falls, 64°19′ W, 53°36′ N, 16 Sep. 1970, *G. R. Brassard 5015* (MICH), 25 Sep. 1970, *5324* (MICH), 6 Jun. 1971, *6154* (H); Thomas Falls, 23 Aug. 1971, *G. R. Brassard 6638* (H). Newfoundland: Fleur de Lys and vicinity, 56° 08′ W, 50°07′ N, 5 Jul. 1976, *G. R. Brassard 11122* (H, MICH); Fortune Bay, 54°39′ W, 47°42′ N, 22 Jun. 1975, *G. R. Brassard 10171* (MICH); middle reaches of stream which enters East Arm at Rocky Cove, 13 Aug. 1977, *A. J. Fife 2805* (MICH). Northwest Territories: Great Bear Lake, McDonough Lake, Jul. 1948, *W. C. Steere 10225* (H, MICH), Hunter Bay, 31 Jul. 1948, *10637* (H, MICH); Mackenzie Distr., Lower Ross Lake, 19 Aug. 1961, *T. Ahti 14657* (H3150695, 3150696); the Taltson River region, 22 Jul. 1962, *G. W. Scotter 2053* (MICH). Nunavut:

Nueltin Lake, Windy Bay, 17 Jul. 1947, *F. Harper 2327* (MICH). Ontario: Kenora Distr., 11 Jul. 1982, *D. H. Vitt s.n.* (H, MICH). Quebec: Lac A L'eau Claire, 13 Jul. 1983, *R. R. Ireland 20898* (MICH); Richmond Gulf, 5 Jul. 1939, *J. Macoun M342* (MICH), 2 Aug. 1939, *M389* (MICH); Ungava Bay, 25 Jul. 1975, *D. Weber 1401* (H); s. loc., 26 Apr. 1891, *J. Macoun 40* (S). Yukon: Hess Mts, 8 Jul. 1976, *D. H. Vitt s.n.* (H, MICH), 16 Aug. 1978, *W. B. Schofield 70969* (H, MICH), 18 Aug. 1978, *71116* (H, MICH), 16 Aug. 1978, *D. H. Vitt 23494* (H), 18 Aug. 1978, *23586* (H), 19 Aug. 1978, *D. H. Vitt 23648* (H); Southern Ogilvie Mts., 19 Jul. 1975, *D. H. Vitt 13479* (H).

China. Xinjiang: Altai Mt., Hanasi Nature Reserve, 3 Aug. 1998, *M. Sulayman K151* (PE), 21 Aug. 2006, *1386* (PE), 29 Aug. 2006, *2287* (PE).

Finland. Central Finland: Päijäne, 1864, *F. Silén s.n.* (H). Kymenlaakso: Pyhtää, 25 Aug. 1967, *V. Kujala s.n.* (H4245197, 4245199), 6 Oct. 1967, *s.n.* (H). Lapland: Enare, 13 Jul. 1880, *A. Arrhenius s.n.* (H), Sep. 1869, *F. Silén s.n.* (H); Kittilä, 13 Aug. 1877, *Hjelt & Hult s.n.* (H). Northern Ostrobothnia: Pudasjärvi, 23 Jun. 1883, *V. F. Brotherus s.n.* (H). Northern Savonia: Vehmersalmi, 21 Jun. 1982, *R. Fagerstén 5074* (MICH). Päijänne Häme: Hollola, 22 Jun. 1864, *Sibei & Norl s.n.* (H). Southwest Finland: Turku, Nagu, 20 Jun. 1937, *O. Eklund s.n.* (H), 11 Aug. 1936, *s.n.* (H), Houtskär, 12 Aug. 1937, *s.n.* (H), Korpo, 18 Aug. 1870, *F. E. W. Etfing s.n.* (H), 25 Apr. 1922, *s.n.* (H). South Karelia: Vehkalahti, 15 Jul. 1968, *L. Fagerström s.n.* (H). Southwest Finland: Kustavi, 17 Nov. 1969, *U. Laine s.n.* (H); Sauvo, 20 Jul. 1966, *V. Oittinen s.n.* (H). Uusimaa: Esbo, May 1908, *H. Buch s.n.* (H), 27 Oct. 1963, *J. Suominen & T. Vuorio s.n.* (H); Helsinki, Aug. 1868, *J. A. Palmén s.n.* (H), 14 Aug. 1868, *S. O. Lindberg s.n.* (H); Borgå, 20 Jun. 1909, *V. F. Brotherus s.n.* (H).

France. Grand Est: Rochesson, 2 Nov. 1898, *Diomier* (NSW).

Norway. Buskerud: Hönefoss, Sep. 1889, *N. Bryhn* (NSW). Hedmark: s. loc., 1834, *s.coll.* (H). Oppland: Dovre, 25 Jul. 1881, *R. Hult s.n.* (H), 27 Jul. 1881, *A332* (H); Kongsvold, Sep. 1868, *P. G. Lorentz s.n.* (HBG); Vang, Aug. 1890, *Kausin* (NSW). Rogaland: Rongoberg, Jun. 1865, *Cleve s.n.* (H); Ryfylke, Jul. 1902, *N. Bryhn* (NSW). Sør Trøndelag: Pref. Nidarosiensis, 1836–37, *J. Ångström s.n.* (H); Oppdal, 14 Nov. 1902, *I. Hagen 241* (HBG, MICH).

Russia. Altai: Altai Mts., Karakem River Valley, 89°10′ E, 50°30′ N, 20 Jun. 1989, *M. Ignatov s.n.* (H). Buryatia: East Sayan, 100°07′ E, 52°34′ N, 11 Jul. 2008, *O. M. Afonina & D. Y. Tubanova s.n.* (H). Karelia: Paanajärvi, 18 Aug. 1867, *F. Silén s.n.* (H); Pojakonda, 14 Aug. 1986, *L. Pujmanová s.n.* (H); Kirjavalaks, 24 Jun. 1874, *S. O. Lindberg s.n.* (H). Khabarovsk: Okhotsk Distr., 22 Jul. 2008, *V. A. Bakalin s.n.* (PE); Bureinskij State Nature Reserve, 11 Aug. 1997, *B. C. Tan 97-284* (H). Magadan: Tenkin Distr., 24 Aug. 1976, *L. S. Blagodatskikh s.n.* (H). Murmansk: Kandalaksha Bay, 6 Aug. 1988, *O. A. Belkina and A. J. Likhachev s.n.* (H), Aug. 1872, *V. F. Brotherus 199* (H); Kola Peninsula, 15 Jul. 1927, *V. P. Savicz s.n.* (H). Sakha: Yakutia, 3 Sep. 2000, *E. I. Ivanova s.n.* (H3219142, 3201313). Zabaykalsky: National Park "Alhanai", 7 Jul. 2006, *O. M. Afonina s.n.* (H, UBC); Sohondinskiy Biosphere Reserve, 25 Jul. 2008, *O. M. Afonina s.n.* (H).

Sweden. Ångermanland: Sandsberget, Jul. 1872, *H. W. Arnell s.n.* (H); Högsjö, 18 Aug. 1915, *A. Arvén s.n.* (H), 1 Aug. 1916, *s.n.* (H); Hernon, 28 Jul. 1875, *H. W. Arnell s.n.* (HBG), 9 Jun. 1873, *s.n.* (H). Dalarna: Älvdalen, 2 Jul. 1916,

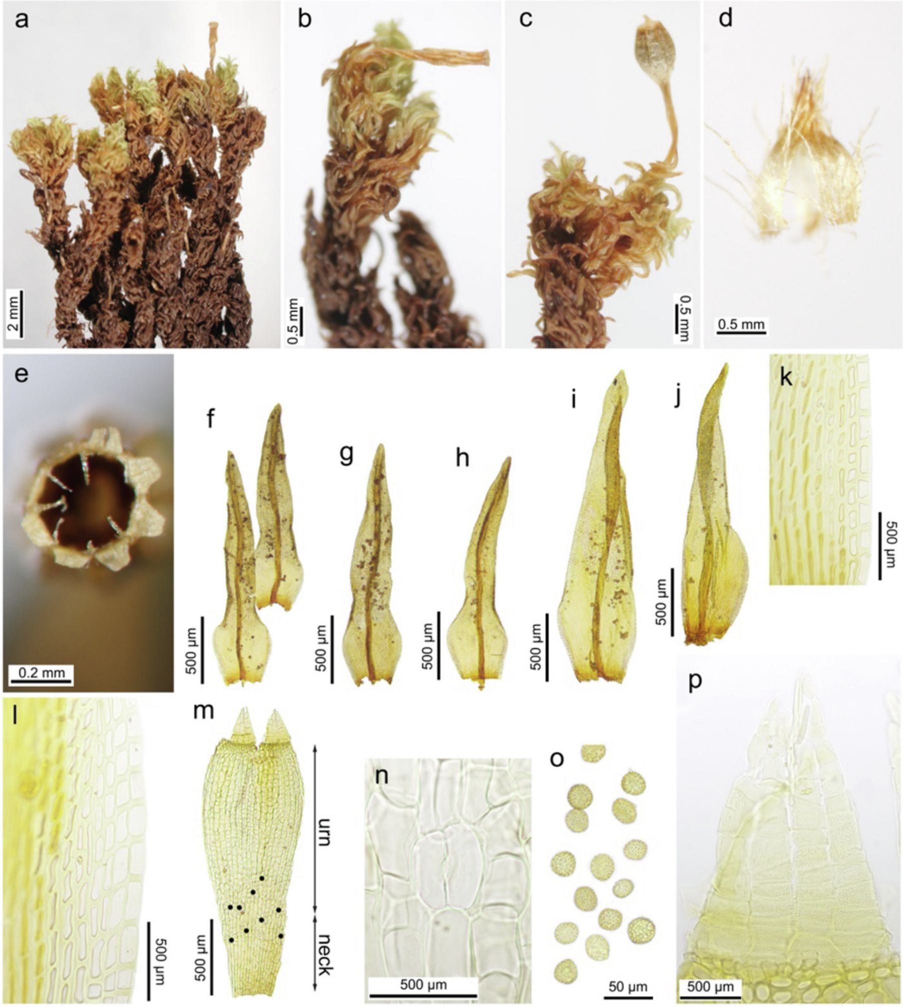


Fig. 50 – *Ulota curvifolia* (Wahlenb.) Lilj. a–b. Habit, with capsules in dry and empty. c. A capsule with operculum. d. Calyptra. e. Capsule mouth viewed from above. f–h. Leaves. i–j. Perichaetial leaves. k–l. Marginal cells at leaf base. m. Exothecial wall, with dots indicating stoma position. n. Stoma. o. Spores. p. Peristome. (a–c and f–p from *M. Sulayman 98-K151* [non-type, PE], d–e from *Afonina s.n.* [non-type, PE]).

G. Samuelsson s.n. (MICH); Frönbergit in Idre, 1859, *P. Olsson s.n.* (H); Idre, Jul. 1893, *L. Jäderholm* (NSW). Hälsingland: Helsingland, 15 Jul. 1909, *H. W. Arnell & C. Jensen s.n.* (H3150718, 3150738, HBG). Härjedalen: Överhogdal, 22 Jun. 1916, *G. R. Cedergren s.n.* (H); Älvros, 29 Jun. 2007, *L. Hedenäs, G. Odelvik & M. Myrdal s.n.* (DUKE); Funäsdalen, 1836, *Thedenius s.n.* (H); s. loc., 1853, *Fristedt et Lovén s.n.* (H). Jämtland: Åre, 6 Aug. 1933, *C. Stenholm s.n.* (H, HBG); Hoverberget,

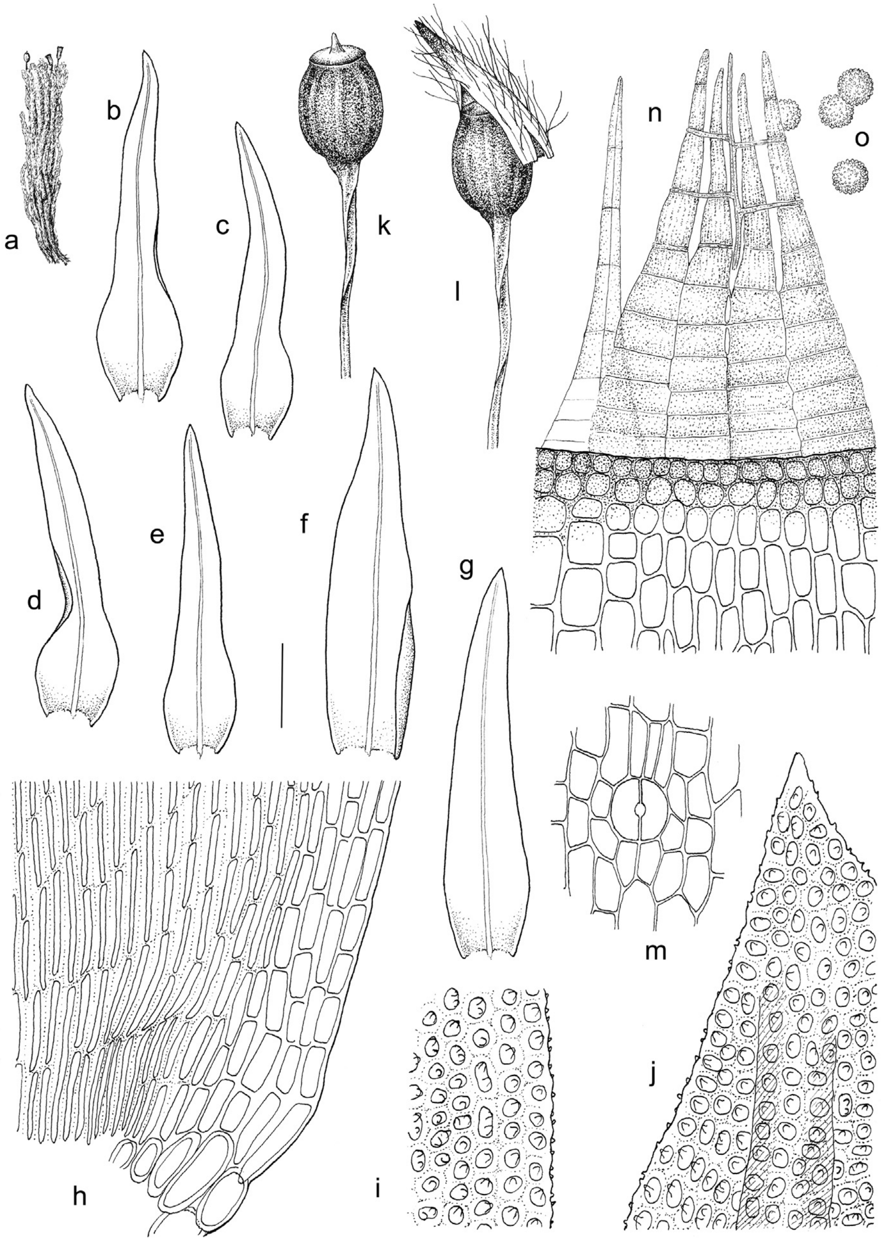


FIG. 51 – *Ulota curvifolia* (Wahlenb.) Lilj. a. plant; b–e. leaves; f–g. perichaetial leaves; h. basal marginal cells; i. median marginal cells; j. top laminal cells; k. a capsule with lid; l. a capsule with calyptra; m. stoma; n. a portion of peristome; o. spores. (Scale bar: a, 10 mm; b–g, 0.48 mm; h–j, 0.04 mm; k and l, 0.77 mm; m–o, 0.05 mm. All drawn from *M. Sulayman K151* [non-type, PE] except calyptra which is from *M. Sulayman 2287* [non-type, PE]).

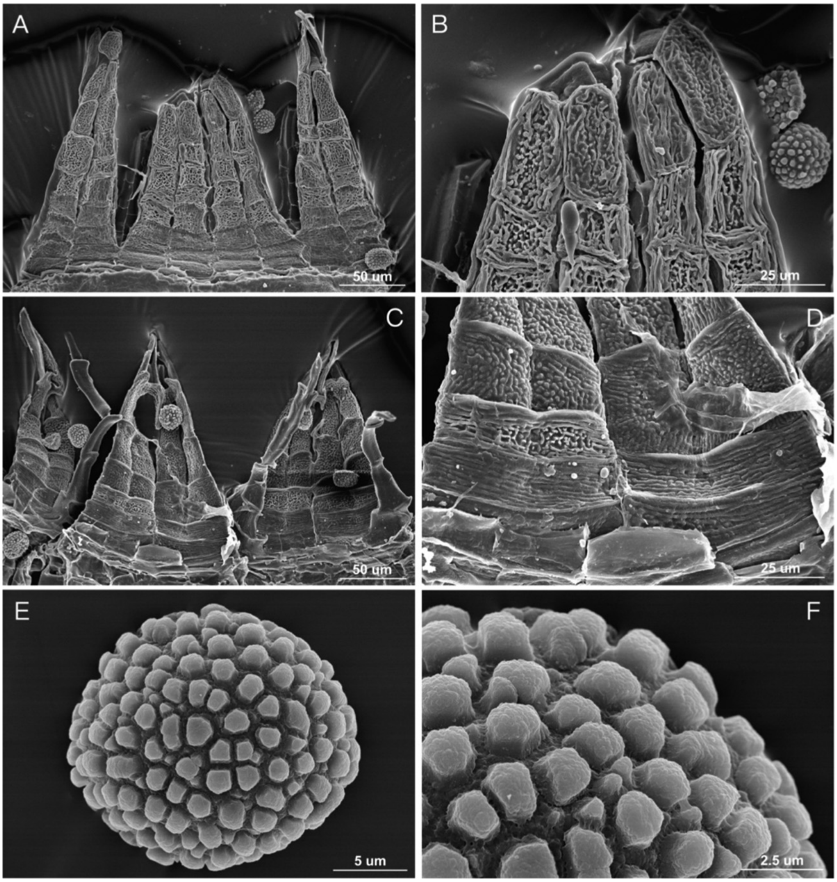


Fig. 52 – *Ulota curvifolia* (Wahlenb.) Lilj. A, outer surface of exostome; B, outer surface of upper exostome; C, inner surface of exostome and endostome; D, inner surface of basal endostome; F, a spore; G, surface ornamentation of a spore. (All from *M. Sulayman K151* [non-type, PE]).

22 Jul. 1904, *A. Grape s.n.* (H); Sundsjö, 20 Jul. 1951, *F. O. Österlind s.n.* (MICH). Lappland: Kvikkjokk, 20 Jul. 1867, *H. Holmgren s.n.* (H); Jalukka Walli, 25 Jun. 1864, *Fredrikson s.n.* (H); Karesuando, 16 Jul. 1912, *H. Möller s.n.* (MICH). Medelpad: Getberget, 20 Jun. 1890, *H. W. Arnell s.n.* (H). Norrbotten: Haaparanda, 1852, *Fristedt et Björnstrand s.n.* (H); Nederluleå, 3 Sep. 1898, *G. H. Hertsön s.n.* (H, MICH); Piteå, Jun. 1856, *S. O. Lindberg s.n.* (H2056060, 2056064), Jul. 1856, *s.n.* (H); Turtola Kynsivaara, 25 Jun. 1877, *Hjelt & Hult s.n.* (H2056065, 3150711, 3150746). Västerbotten: Åsele, Dorotea, 8 Aug. 1921, *C. Stenholm s.n.* (H).

U.S.A. Alaska: Arctic Coast Distr., 4 Aug. 1958, *S. Shushan & John W. Thomson, Jr.* (S); Bettles Quad, 27 Jul. 1982, *J. Lewinsky 2745* (MICH); Brooks

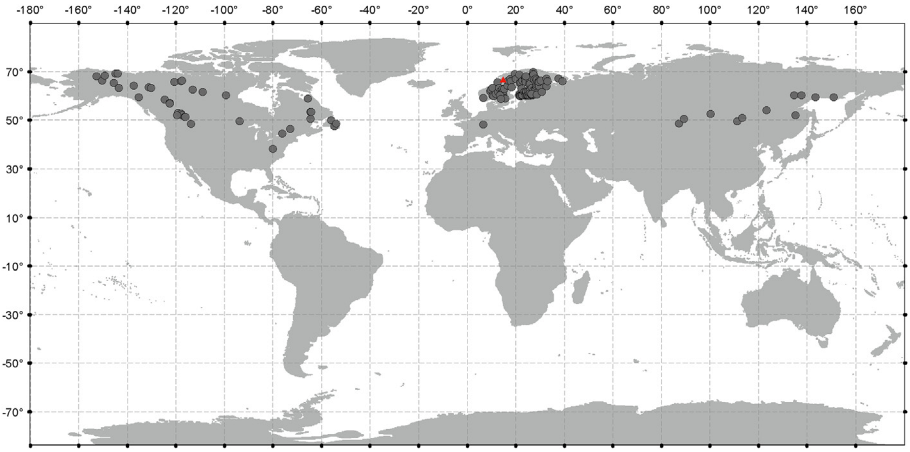


Fig. 53 – Distribution of *Ulota curvifolia* worldwide. The red triangle indicates the type locality.

Range, Peters Lake, 21 Jul. 1960, *W. C. Steere, K. A. Holmen and O. Mårtensson s.n.* (H, MICH), 25–26 Jul. 1965, *W. C. Steere 650726-25* (H), 26 Jul.–2 Aug. 1972, *72-543* (H), 21–25 Jul. 1960, *s.n.* (H), Mountains Northwest of Walker Lake, 18 Aug. 1950, *L. H. Jordal 4054* (MICH), Endicott Mt., 20 Jul. 1952, *W. C. Steere 18332* (H), *18342* (H); Clifton Station, Skagway, 9–12 May 1966, *F. M. Boas 23* (UBC); Pennell Mountain trail at Twelve Mile Summit, 11–25 Sep. 1979, *D. H. Norris 54119* (MICH); Philip Smith Mts Quad, 29 Jul. 1982, *J. Lewinsky 2607* (MICH); Tanana River area, Tetlin National Wildlife Reserve, 27 Jul. 2001, *W. B. Schofield 118317* (DUKE), *118321* (UBC). Virginia: Marlinton, 23 Dec. 1931, *F. W. Gray* (NSW).

11. **Ulota delicata** Q.H. Wang & Y. Jia, Bryologist 115(3): 420. 2012. Type: China. Fujian, Mt. Wuyi, Sangang, roadsides to Xianglufeng, on the pine, alt. 1200 m, 20 Apr. 1955, *bryophyte training class 933-d* (holotype, PE! KUN0878542!).

Plants 1–1.5 cm tall, yellowish green on the top, brown to black below. Stem usually branched. Leaves strongly crisped when dry, patent when moist, (1.6–) 1.9–2.7 (–3.5) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex long acuminate; costae strong, percurrent or ending near the apex. Upper and middle laminal cells round to oblong, (7–) 9–13 (–17) × (6–) 7–8 (–10) μm, thick-walled, with low papillose or nearly smooth; basal inner cells rhomboidal, rectangular to elongate-rectangular, (17–) 22–26 (–31) × (3–) 4–5 (–7), smooth, strongly thickened wall; basal marginal cells differentiated in (3–) 5–9 (–12) rows hyaline band, quadrate to rectangular, with thickened transverse walls.

Autoicous. Perichaetial leaves hardly differentiated, (2–) 2.1–3.2 (–3.4) mm. Vaginula is naked or sparsely hairy. Seta (2–) 3–4 (–4.5) mm long, twisted anticlockwise when dry. Capsules long exserted, 1.5–1.9 (–2.4) mm long. Urn cylindrical to long-cylindrical, often distinctly constricted at the mouth when dry and empty, puckered, 8-ribbed the entire length. Neck short or slightly long, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, four to five cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction of urn and neck. Preperistome is rarely present. Peristome double. Exostome teeth 16, united into 8 pairs, variably erect or spreading to recurved when dry, lanceolate, throughout strongly and densely papillose, sometimes striolate-papillose inside. Endostome segments 16 (8 often alternately caducous), filiform, fragile, no more than 2/3 height of teeth, hyaline, finely papillose. Opercula with a short beak. Calyptra mitrate, densely hairy. Spores globose, finely papillose, (20–) 26–35 (–41) μm in diameter.

Illustration: Wang and Jia (2012a); figures 54 and 55.

Habitat: It grows on branches or trunks of trees, only two records from pine. There are some altitude records: (860–) 1200–2160 (–3120) m. It's often mixed with *U. crispa*, *U. gymnostoma* and *U. latisegmenta*.

Distribution: It is **endemic** to East Asia, including China and Japan, for which the latter is the first record. Figure 56.

Notes: The main diagnostic characteristics of *Ulota delicata* are strongly crisped leaves, cylindrical capsules with puckered mouth, and 16 filiform endostome segments.

Ulota delicata is similar to *U. drummondii* in the well-differentiated hyaline cells in basal leaf margins, capsules with puckered mouth and exostome teeth with strongly and densely papillose throughout, but the latter differs in the flexuose leaves, absent endostome segment and relatively small spores (24–27 μm). *Ulota delicata* is also close to *U. crispa* in the strongly crisped leaves and the cylindrical capsules, but the latter is distinguished by the non-puckered capsule mouths, narrow-lanceolate endostome segments (not fragile), and relatively weakly ornamentated peristome.

No noteworthy variation was observed in *Ulota delicata*.

Key to *Ulota delicata* and its closely related species.

1. Capsules without puckered mouth when dry; endostome segments narrow-lanceolate, not fragile; peristome relatively weakly ornamentated....... *U. crispa*
1. Capsules with puckered mouth when dry; endostome segments absent or filiform, fragile; peristome strongly ornamentated... 2
2. Leaves erect to flexuose when dry; endostome segment absent or rudimentary; spores relatively small, 24–27 μm... *U. drummondii*
2. Leaves strongly crisped when dry; endostome segments 16, filiform; spores large, 31–37 μm.. *U. delicata*

Additional specimens examined: **China**. ANHUI: Huangshan city, Tunxi, Huashan Hotel, 20 May 1982, *Q. Gao s.n.* (IFP), Yellow Mt., 18 Aug. 1961, *Z.-L. Wan & J.-X. Luo 9226* (PE), 25 Apr. 1957, *P.-C. Chen et al. 6801c* (PE), 27 Apr. 1957, *7047b* (PE). FUJIAN: Wuyi Mt., 20 Apr. 1955, *Bryophyte training class 933-b* (KUN), 27°51′34″ N, 117°46′58″ E, 26 May 2015, *W.-Z. Ma 15-6417* (PE). GUANGXI: Xingan

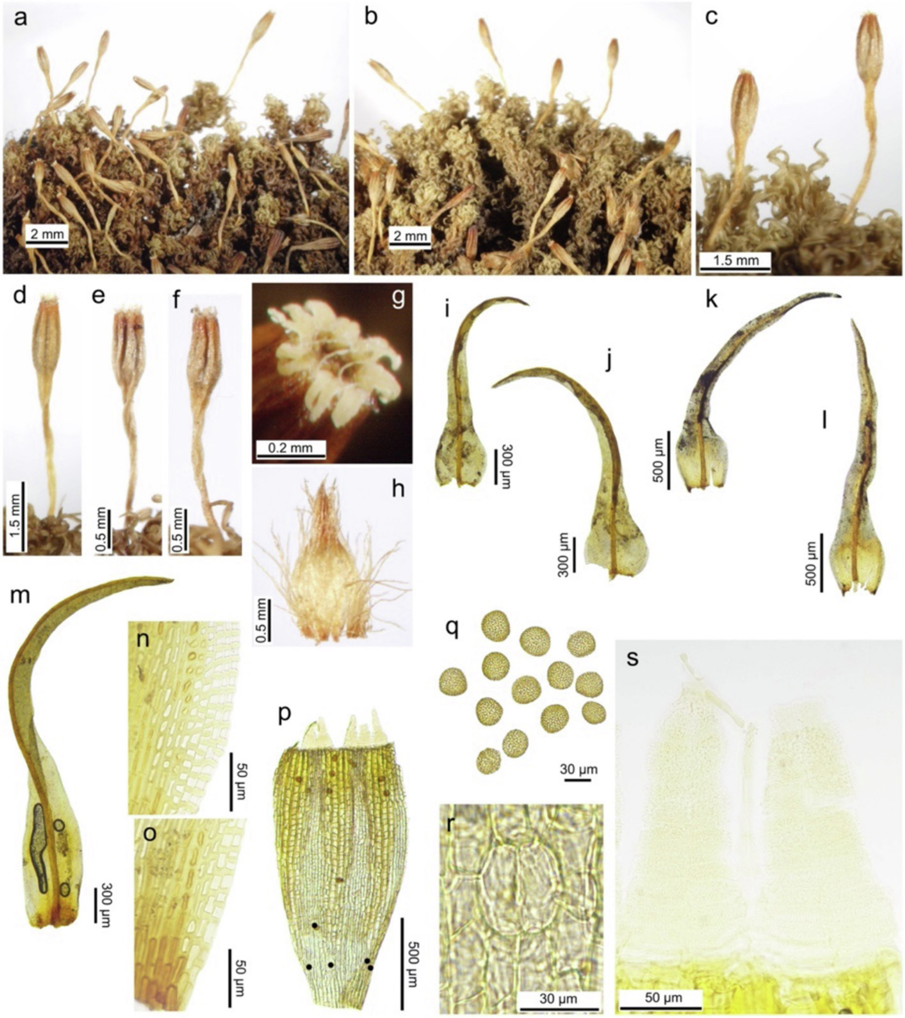


Fig. 54 – *Ulota delicata* Q.H. Wang & Y. Jia. a–b. Habit. c–f. Capsules in dry and empty. g. Capsule mouth viewed from above. h. Calyptra. i–l. Leaves. m. Perichaetial leaf. n–o. Marginal cells at leaf base. p. Exothecial wall, with dots indicating stoma position. q. Spores. r. Stoma. s. Peristome. (All from the holotype in PE).

Co., Maoer National Nature Reserve, 7 Sep. 2018, *S. He & Y.-M. Wei 48647* (IBK), 30 Mar. 2019, *Q.-M. Tang et al. 20190330-50* (IBK); Ziyuan Co., Chetian, Shiwangutian, 19 Jun. 2021, *Q.-M. Tang 20210619-20* (IBK). Guizhou: Jiangkou Co., Fanjing Mt., 28 Jul. 1983, *Q. Gao 32295* (IFP, PE), 30 Jul. 1983, *32582* (IFP), *32607* (PE); Leishan Co., Leigong Mt., 24 Jul. 1980, *S.-Z. Jiang 10347* (IFP); Suiyang Co., Kuankuoshui, 1982, *Q.-W. Lin yibo-168* (PE). Hunan: Wugang, Yunshan, 25 Jun. 1992, *T. Cao & X. Fu 42377* (IFP). Zhejiang: Pinghu, Jiulong Mt., 5 May 1981, *Z.-L. Liu 1116* (PE).

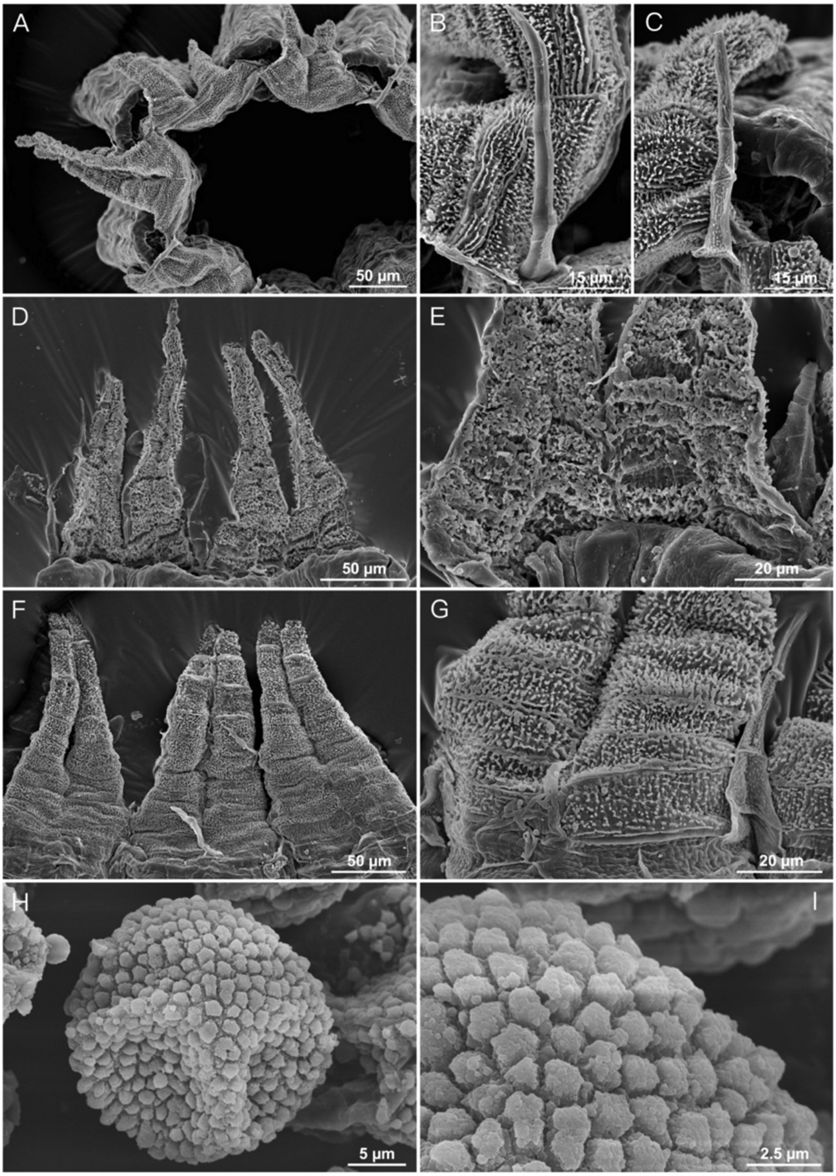


FIG. 55 – *Ulota delicata* Q.H. Wang & Y. Jia. A, capsule mouth; B, outer surface of endostome; C, inner surface of endostome; D, outer surface of exostome; E, outer surface of basal exostome; F, inner surface of exostome; G, inner surface of basal exostome; H, spores; I, surface ornamentation of a spore. (All from *Q. Gao* [non-type, IFP]).

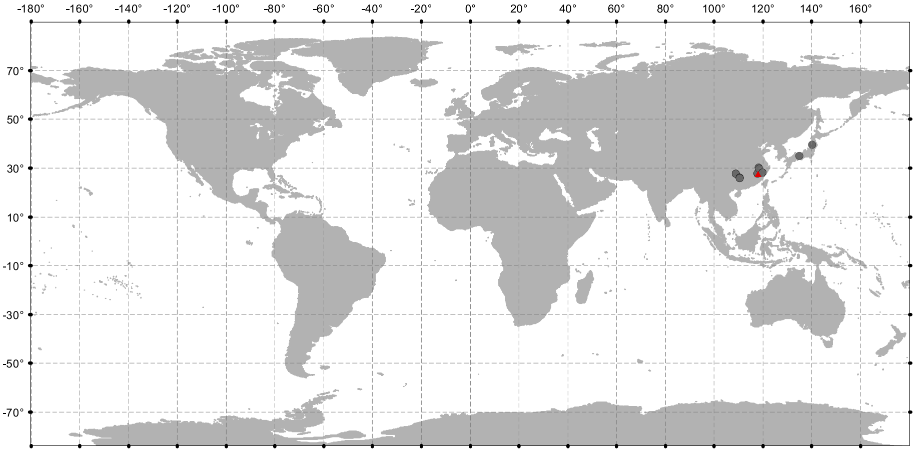


Fig. 56 – Distribution of *Ulota delicata* worldwide. The red triangle indicates the type locality.

Japan. Akita: Lake Tazawa, 28 Jul. 1996, *Y. Takahashi YT-11086* (AKPM). Hyogo: Yabu-gun, 20 Aug. 1956, *S. Nakanishi 11* (HYO), *47 (417)* (HYO).

12. **Ulota drummondii** (Hook. & Grev.) Brid., Bryol. Univ. 1: 299. 1826. ≡ *Orthotrichum drummondii* Hook. & Grev., Scott. Crypt. Fl. 2: 115. 1824. ≡ *Macromitrium drummondii* (Hook. & Grev.) Hampe, Flora 20: 280. 1837. ≡ *Ulotrichum drummondii* (Hook. & Grev.) Schimp., Bryologia Europaea 3: 1 (fasc. 46–47 Consp. vol. 3: I). 1851. *invalid, genus invalid.* ≡ *Weissia drummondii* (Hook. & Grev.) Lindb., Journal of Botany, British and Foreign 11: 200. 1873. Type: U.K. Scotland, near Forfar, Glen Fallach, 1823, *T. Drummond 60* (lectotype, E00052663-66! designated by Wang and Jia, 2012a).

Orthotrichum subrepens Sommerf., Supplementum Florae Lapponicae 191. 1 f. 2. 1826. Type: "Alnorum Nordlandiae saltensis".

Ulota bicolor Bridel, Bryologia Universa 1: 792. 1827. Type citation: "In insulà Terre Neuve arborum cortici adrepens et adeo tenaciter adhaerens ut vix illaesa separari queat, densissime caespitosa habitat. Clar. La Pylaie detector nos illius compotes fecit." (holotype, B).

Ulota funstonii Grout, Moss Flora of North America 2: 137. pl. 57: A. 1935. Type: U.S.A. Alaska, Yakutat Bay, *Funston 158* (holotype, US).

Ulota japonica var. *stenocarpa* Cardot, Bull. Herb. Boissier, sér. 2, 8: 336. 1908. Type: Japan. Kuroishi, *Faurie 2643* (syntype, KYO).

Plants 0.5–2 cm tall, yellowish green to green above, brown to black below. Stems usually branched. Leaves erect to strongly flexuose, rarely crisped when dry, patent when moist, (1.3–) 1.8–2.6 (–3.4) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex long acuminate; leaf margin plane; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, (7–) 10–13 (–15) × (5–) 7–10 (–14) μm, thick-walled, with low simple papillae or nearly smooth; basal inner cells linear, rectangular to vermicular, (20–) 27–40 (–55) × (2–) 3–5 (–8) μm, with strongly thickened wall, smooth; basal marginal cells differentiated in (2–) 4–6 (–10) rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves somewhat longer, (2.2–) 2.8–3.2 (–3.5) mm. Vaginula is somewhat hairy or naked. Seta (3–) 3.5–4 (–4.5) mm long, twisted anticlockwise when dry. Capsule long exserted, (1.7–) 2.1–2.5 (–2.7) mm long. Urn long, cylindrical, or narrow fusiform, distinctly constricted when dry and empty, forming the somewhat puckered mouth, eight furrows along the entire length, with prominent ribs alternately. Neck long when the capsule is empty, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, two to three cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the transition zone between urn and neck. Preperistome is not seen. Peristome often single. Exostome teeth 16, often united into 8 pairs, flexuose to variably recurved when dry, hardly lying on the exothecium, lanceolate, densely and coarsely papillose on both sides. Endostome segments are absent, rarely rudimentary, with one or two cells of height, hyaline, and scabrous on the inside surface. Opercula often with a long beak. Calyptra mitrate is covered by many long hairs. Spores spherical, finely papillose, (19–) 24–27 (–30) μm in diameter.

Illustration: Nyholm (1960), Smith (1978), Crum and Anderson (1981), Noguchi and Iwatsuki (1989) and Wang and Jia (2012a); figures 57 and 58.

Habitat: It only grows on trunks or branchs of trees, such as *Abies*, *Alnus* (alder), *Betula* (birch), *Crataegus*, *Corylus* (hazel), *Fraxinus*, *Juniperus*, *Populus*, and *Salix*. There are some records of altitude: (5–) 130–396 (–600) m. It usually grows together with *U. crispa*, sometimes with *U. coarctata* and *U. phyllantha*.

Distribution: It is common to the coastal area in the northern hemisphere. Figure 59.

Notes: *Ulota drummondii* is distinguished by its erect to flexuose leaves, well-differentiated hyaline cells in basal leaf margins, long cylindrical capsules with puckered mouth, and absent endostome segment.

Ulota drummondii is similar to *U. hutchinsiae* in the non-crisped leaves when dry, but the latter differs in erect-appressed leaves, hardly differentiated leaf basal marginal cells (no more than three rows), capsules without puckered mouth, well-developed endostome segments, smaller spores (13–14 μm) and saxicolous habit. *Ulota drummondii* also resembles *U. delicata* from China in well-differentiated hyaline cells in basal leaf margins, capsules with the puckered mouth when dry, and exostome teeth with densely and coarsely papillose throughout. *Ulota delicata*, however, differs in strongly crisped leaves, 16 filiform endostome segments, and relatively large spores (31–37 μm).

No noteworthy variation was observed in *Ulota drummondii*.

Key to *Ulota drummondii* and its closely related species.

1. Leaves strongly crisped when dry; spores large, 31–37 μm................*U. delicata*
1. Leaves erect to flexuose when dry; spores small, 13–27 μm..............................2
2. Leaves erect-appressed when dry; leaf basal marginal cells hardly differentiated (no more than three rows); capsules without puckered mouth when dry; endostome segments well-developed, eight; spores smaller, 13–14 μm; rock-growing..*U. hutchinsiae*
2. Leaves erect to flexuose when dry; leaf basal marginal cells well differentiated (4–6 rows); capsules with puckered mouth when dry; endostome segment absent or rudimentary; spores relatively large, 24–27 μm; tree-growing..*U. drummondii*

Additional Specimens Examined: **Canada**. British Columbia: Prince Rupert area, 13 Nov. 1964, F. *M. Boas 36-2* (UBC); Skeena River area, 10 Sep. 1964, *W. B. Schofield 25704* (UBC). Newfoundland: Alpine Plateau, Gros Morne National Park, 11 Sep. 1980, *R. J. Bellan 3912* (H, MICH), *3915-2* (MICH), 26 Jul. 1977, *A. J. Fife 2368* (MICH); Avalon Peninsula, 53°38′ W, 47°15′ N, 9 Sep. 2007, *B. Allen 28657A* (MO), 10 May 1976, *G. R. Brassard 10614* (H, MICH), Butterpot Provincial Park, 2 Jul. 1966, *D. H. Norris 3562* (MICH); Ferryland Distr., Biscay Bay, 7 Jun. 1949, *R. Tuomikoski 544* (H), 9 mi WSW of Tor's Cove, 18 May 1956, *T. Ahti 9431* (H3150763, 3150764); Burgeo-La Poile Distr., 21 Jun. 1949, *R. Tuomikoski 1345a* (H); Humber East Distr., 26 Jun. 1956, *T. Ahti 7904* (H); Port au Port Distr., 2–4 Jul. 1949, *R. Tuomikoski 2379* (H), 8–9 Jul. 1949, *R. Tuomikoski 2798a* (H); St. Barbe Distr., Cow Head, 10 Aug. 1949, *R. Tuomikoski 5039* (H); ca. 1 mi. W. of junction of Lomond Rd. and Prov. Hwy. 44, 15 July 1966, *D. H. Norris 4309* (MICH).

Finland. Aland: Sonroda, 20 Sep. 1865, *J. O. Bomansfon* (NSW).

France. Bretagne: La Roche-Maurice, May 1894, *L. Bason 104-2* (NSW).

Ireland. Connacht: Roscommon Co., Elphin, 29 Aug. 1860, *J. A. F. & A. J. E. Smith s.n.* (E).

Japan. Akita: 17 Oct. 1980, *Y. Takahashi YT-5653* (AKPM); Yamatoto, 17 Sep. 1993, *M. Higuchi 32011-1* (TNS). Hidaka: Nissho Pass, *Z. Iwatsuki 682* (TNS); Mt. Poroshiri, *Z. Iwatsuki 518* (TNS). Hokkaido: Kushiro Twp., 21 Sep. 2003, *W. B. Shofield 122394-2* (UBC); Hidaka, 27 Jul. 1971, *Z. Iwatsuki 518-2* (TNS), 31 Jul. 1971, *Z. Iwatsuki 682-1* (TNS). Tochigi: Mt. Shirane, 9 Sep. 1999, *M. Higuchi s.n.* (PE, BISH, MICH).

Norway. Hordaland: Stard, 26 Aug. 1931, *M. J. Kotilainen s.n.* (H), 31 Aug. 1927, *s.n.-1* (H). Møre og Romsdal: Volda, 31 Jul. 1920, *M. J. Kotilainen s.n.-2* (H). Nordland: Helgeland, 4 Jul. 1870, *H. W. Arnell s.n.* (MICH); Torghattan, 22 Aug. 1911, *M. Fürbrenger s.n.* (H). Rogaland: Stavanger, Jul. 1902, *N. Bryhn* (NSW). Sør Trøndelag: Gjejkfield, 19 Oct. 1890, *I. Hagen* (NSW); Trondheim, 1890, *J. H. s.n.* (HBG), *J. Ångström s.n.* (H), 1837, *s.n.* (H), Jul. 1907, *N. Bryhn s.n.-1* (NSW), 1889, *J. Hagen s.n.* (H), 19 Oct. 1890, *s.n.* (H).

Russia. Kamchatka: Statio, middle Bannaya River, 157°30′ E, 52°54′ N, 6 Aug. 2002, *I. V. Czernyadjeva 46* (H). Sakhalin: Iturup Island, 147°34′30.2″ E,

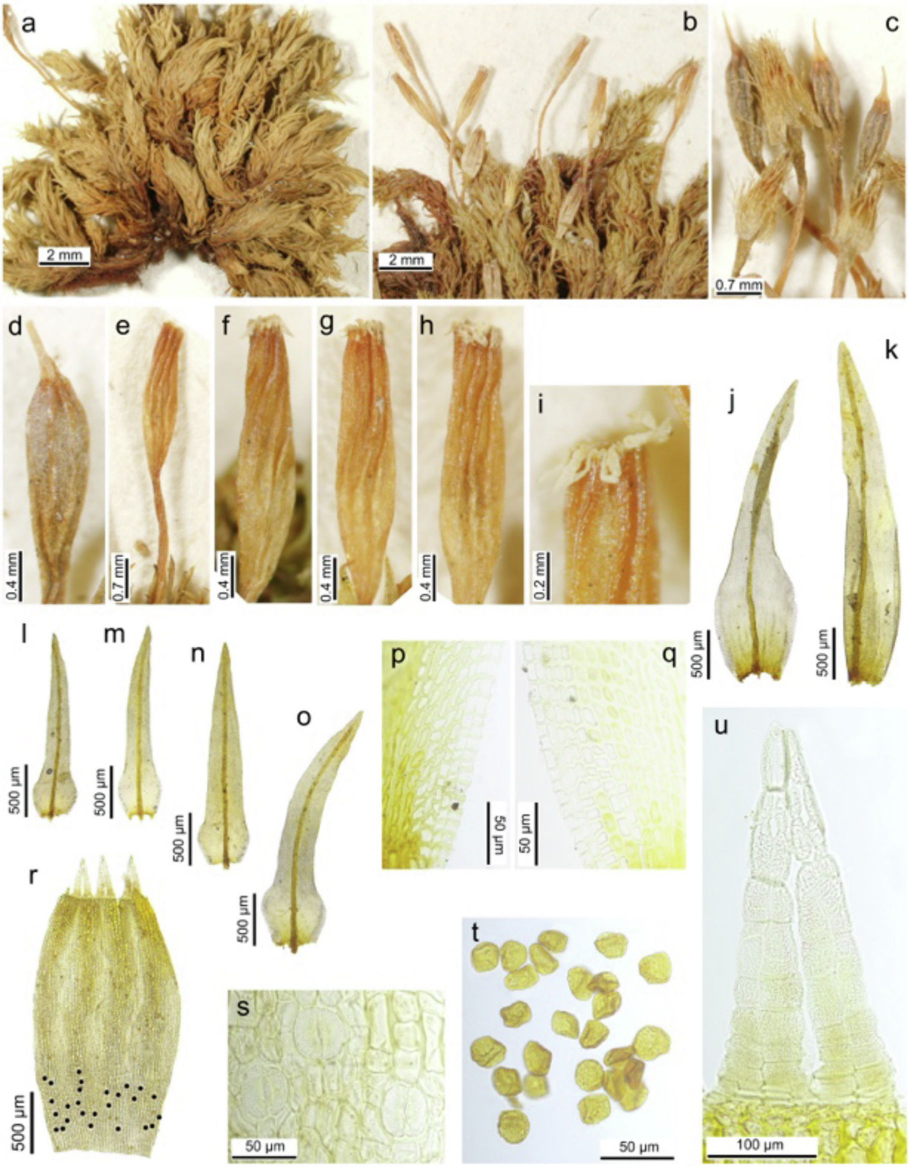


FIG. 57 – *Ulota drummondii* (Hook. & Grev.) Brid. a–b. Habit. c. Calyptra. d–h. Capsules in dry. i. Puckered capsule mouth. j–k. Perichaetial leaves. l–o. Leaves. p–q. Marginal cells at leaf base. r. Exothecial wall, with dots indicating stoma position. s. Stomata. t. Spores. u. Peristome. (All from the lectotype in E).

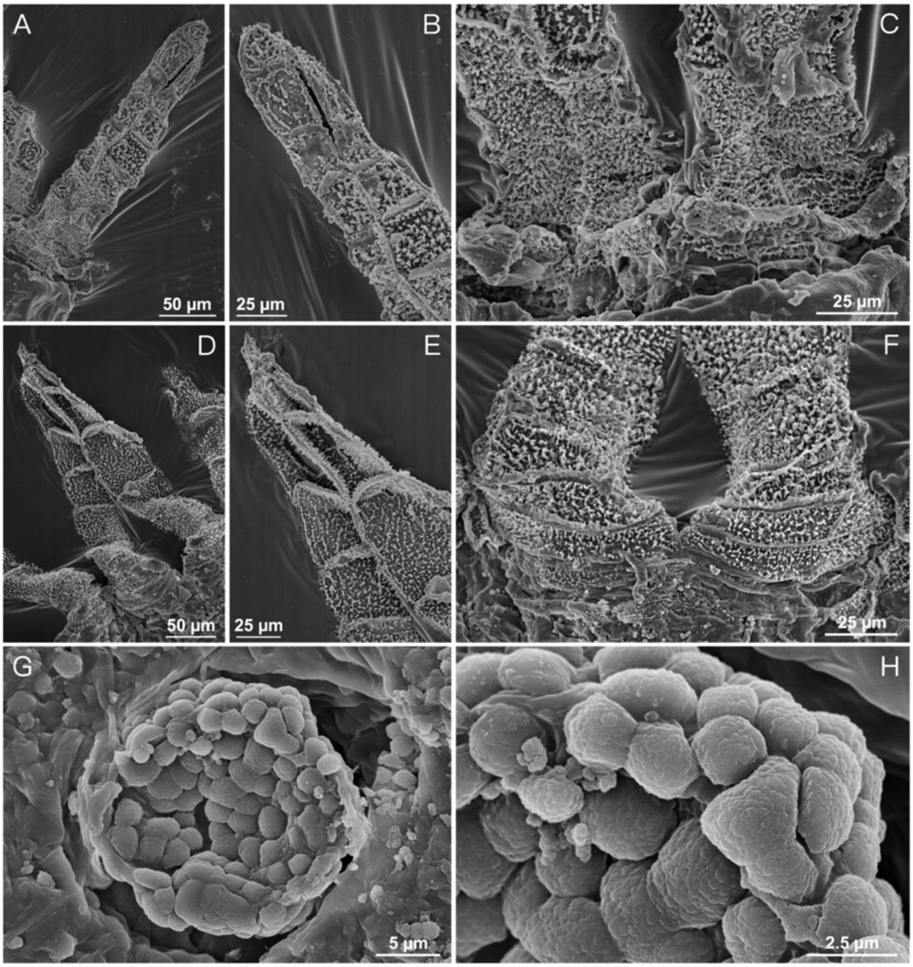


FIG. 58 – *Ulota drummondii* (Hook. & Grev.) Brid. A, outer surface of exostome; B, outer surface of upper exostome; C, outer surface of basal exostome; D, inner surface of exostome; E, inner surface of upper exostome; F, inner surface of basal exostome; G, a spore; H, surface ornamentation of a spore. (All from the lectotype in E).

44°55′55.6″ N, 7 Aug. 2007, *V. A. Bakalin s.n.* (PE); Kunashir Island, 13 Aug. 1978, *V. Y. Cherdantseva s.n.* (PE).

Sweden. DALSLAND: s. loc., 5 May 1934, *G. Svensson s.n.* (H). NÄRKE: s. loc., 2 Jun. 1884, *E. Adlerz s.n.* (H), 5 Oct. 1884, *s.n.* (H); Hidinge, 9 Jun. 1854, *s.n.* (H). VÄSTER-GÖTALAND: Halland, 6 Jun. 1933, *C. Stenholm s.n.-2* (MICH). VÄSTMANLAND: Viker, 18 Aug. 1966, *T. Koponen 10692* (H).

U.K. ENGLAND: Teesdale, 7 Jul. 1843, *Spruce s.n.* (H). SCOTLAND: Aberdeenshire, 17 Aug. 1836, *W. Wilson s.n.* (MICH); Argyll, 28 May 1970, *A. C. Crunowell s.n.* (E), 6 Sep. 1972, *C. C. Townsend 72/279* (E), 1 May 1999, *D. G. Long 28334* (E);

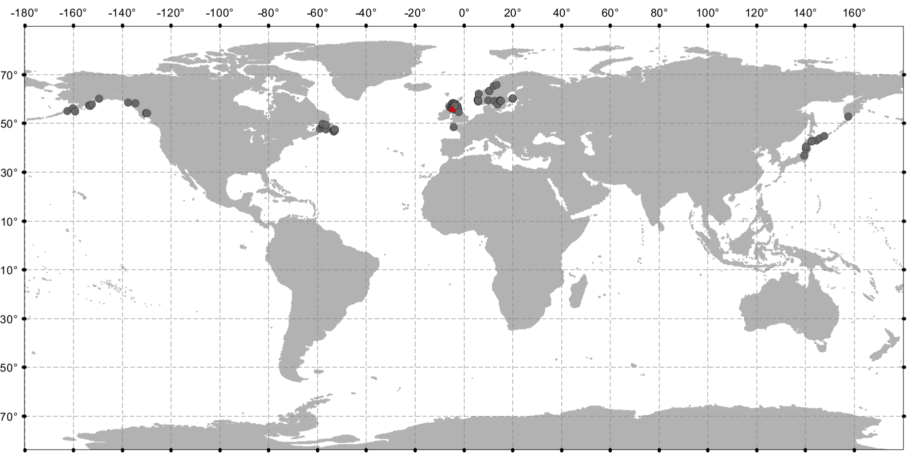


FIG. 59 – Distribution of *Ulota drummondii* worldwide. The red triangle indicates the type locality.

Berwickshire, 14 May 1989, *D. G. Long 16095* (E), 23 Mar. 1992, *21844* (E), *21863* (E), 14 Feb. 1993, *23287* (E), 10 May 1999, *28392* (E); Easterness, Aviemore, 10 Sep. 1860, *J. A. Paton s.n.* (E), Jun. 1951, *U. Dunczn s.n.* (E), 22 Jul. 1956, *C. C. Townsend 560722/15* (E), 27 Jul. 1956, *560727/34* (E), 11 Aug. 2001, *D. G. Long 30198* (E), 25 Sep. 2003, *D. G. Long 32153* (E), 13 Jun. 2004, *D. F. Chamberlain s.n.* (E), 4 Jul. 2010, *39417* (E); East Inverness, 24 Jun. 2005, *D. F. Chamberlain s.n.* (E); East Lothian, 25 Apr. 1994, *D. G. Long 25309-1* (E), 18 Jul. 1999, *D. F. Chamberlain s.n.* (E); East Sutherland, 5 Jul. 2006, *D. F. Chamberlain & E. M. Kungu s.n.* (E); Highland, Creag Shomhairle, 24 Jun. 1974, *D. F. Chamberlain & D. G. Long s.n.* (E); Lanarkshire, 16 May 2009, *D. F. Chamberlain & E. M. Kungu s.n.* (E); Loch Garry, 11 Apr. 1971, *D. G. Long 1282-1* (E); Loch Katrine, 11 Jul. 1868, *Hunt s.n.* (H); Loch Moidart, 10 Apr. 1974, *D. G. Long 3321* (E); Sutherland, 8 Jul. 1899, *H. N. Dixon s.n.* (E), 31 Aug. 1960, *A. C. Crunowell & E. F. Wertwig s.n.* (E); Selkirkshire, 5 Mar. 2013, *D. G. Long & J. Smith 42322* (E); Strathnaver, 4 Jul. 1867, *H & M Corley s.n.* (E); Westerness, 11 Jun. 1990, *D. G. Long 18241* (E).

U.S.A. ALASKA: Auke Village Recreation area, 7 Aug. 1967, *F. J. Hermann 22126* (MICH); Falls Creek and Blunt Mountain, 17–18 Jul. 1969, *I. A. Worley & G. Streueler 13035-1* (UBC); Izembek National Wildlife Reserve, 5 Aug. 1977, *W. B. Schofield 108950-2* (UBC), 29 Jul. 1993, *99624-1* (UBC); Kenai Peninsula Co., 2 Sep. 2006, *W. B. Schofield 125413* (UBC); Kodiak Island, 8 Jun. 1968, *A. J. Sharp 10* (UBC), 2 Aug. 1994, *W. B. Schofield 101169A* (DUKE), May 1938, *E. H. Looff E162-1* (MICH), *E189* (MICH); Sandy River, 6 Jul. 2000, *W. B. Schofield 114684* (DUKE); Simeonof Island, 11 Jul. 1996, *W. B. Schofield 105895* (UBC); Sitkalidak Island, Aug. 1931, *W. J. Eyerdam 5* (MICH); s. loc., 20 Aug. 1944, *A. M. Harvill, Jr. 506* (MICH).

13. **Ulota ecklonii** (Hornsch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 163. 1874. ≡*Orthotrichum ecklonii* Hornsch., Linnaea 15: 129. 1841. Type: South Africa. Cape Tafelberg, *Ecklon s.n.* (holotype, BM000868281! isotypes, S-B157873! PRE778432!).

Plants 1–1.5 cm tall, yellow to green above, brown to black below. Stems usually branched. Leaves strongly crisped when dry, erect-patent when moist, (1.2–) 1.7–2.4 (–2.8) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex long acuminate; leaf margin plane or irregularly partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, (8–) 10–12 (–16) × (6–) 8–10 (–12) μm, thick-walled, with low simple papillose; basal inner cells linear, rectangular, elongate-rectangular to vermicular, (14–) 22–29 (–37) × (4–) 6–7 (–9) μm, with moderately thickened wall, smooth; basal marginal cells distinctly differentiated in 4–8 rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves much longer, (2.6–) 3.1–3.5 (–3.7) mm. Vaginula naked. Seta ca. 2.5 mm long, slightly twisted anticlockwise when dry. Capsule long exserted, (1.5–) 1.6–1.7 mm long. Urn cylindrical strongly constricted below the mouth when dry and empty, with eight furrows along the entire length, with prominent ribs alternately. Neck slightly long, gradually narrowed to the seta. Exothecial cells differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, scattered on the central or lower part of the urn. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, often lying on the exothecium, lanceolate, reticulate striate on the outside, striate above, and smooth below on the inside. Endostome segments 8, linear-lanceolate, ca. 1/4 width of teeth in the middle, almost as tall as exostome, hyaline, variably incurved when dry, smooth on both sides. Opercula not seen. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (23–) 26–32 (–38) μm in diameter.

Illustration: Magill and van Rooy (1998); figures 60 and 61.

Habitat: There is only one record from sandstone. Two records of altitude: 1000–1200 m.

Distribution: It is **endemic** to and rare in Africa, including South Africa and South Sudan. Figure 62.

Notes: The remarkable characteristics of *Ulota ecklonii* are the reticulate-striate exostome teeth and urn-located stomata.

It is similar to widespread *Ulota crispa* and South American *U. germana*. They all have strongly crisped leaves, distinctly differentiated cells at basal leaf margins, strongly constricted capsules, eight narrow endostome segments, and densely hairy calyptra. However, *Ulota crispa* differs in the stomata on the transition zone between urn and neck, exostome teeth often with papillose outside, often scabrous endostome teeth, often longer seta (3–5 mm), more rows (5–11) of hyaline cells at basal leaf margins and smaller spores (19–25 μm), while *U. germana* differs in the perichaetial leaves often prominently sheathing around the seta, and the often papillose peristome.

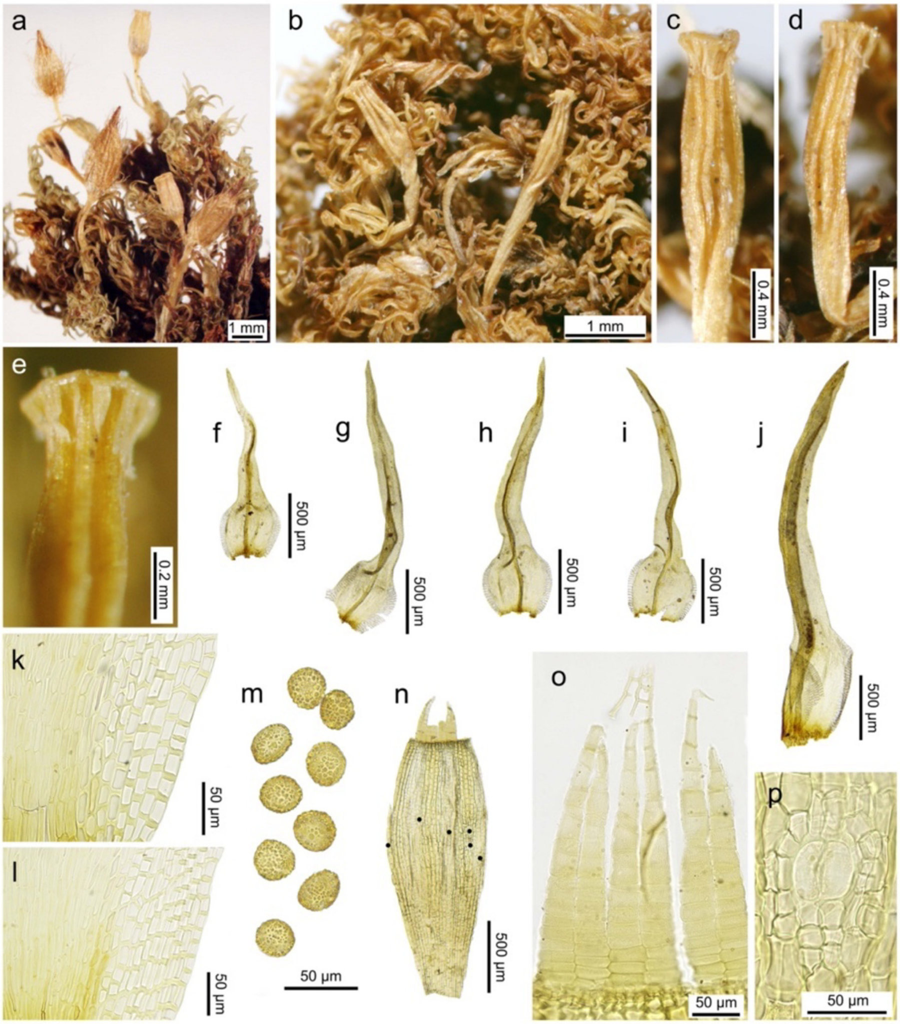


FIG. 60 – *Ulota ecklonii* (Hornsch.) A. Jaeger. a–b. Habit. c–d. Capsules in dry and empty. e. Constricted capsule near mouth. f–i. Leaves. j. Perichaetial leaf. k–l. Marginal cells at leaf base. m. Spores. n. Exothecial wall, with dots indicating stoma position. o. Peristome, with endostome segments missing. p. Stoma. (All from the isotype in S except a from *Thorne 3638* [non-type, PRE]).

Key to *Ulota ecklonii* and its closely related species.

1. Stomata on the junction between urn and neck; seta longer, 3–5 mm; spores small, 19–25 μm..*U. crispa*
1. Stomata on the central or lower part of urn, sometimes on the junction between urn and neck; seta shorter, 1.7–2.9 mm; spores larger, 26–35 μm....................2

2. Exostome teeth often papillose outside; perichaetial leaves often prominently sheathing around the seta; endostome segments often papillose....... *U. germana*
2. Exostome teeth reticulate-striate outside; perichaetial leaves not prominently sheathing around the seta; endostome segments smooth.................. *U. ecklonii*

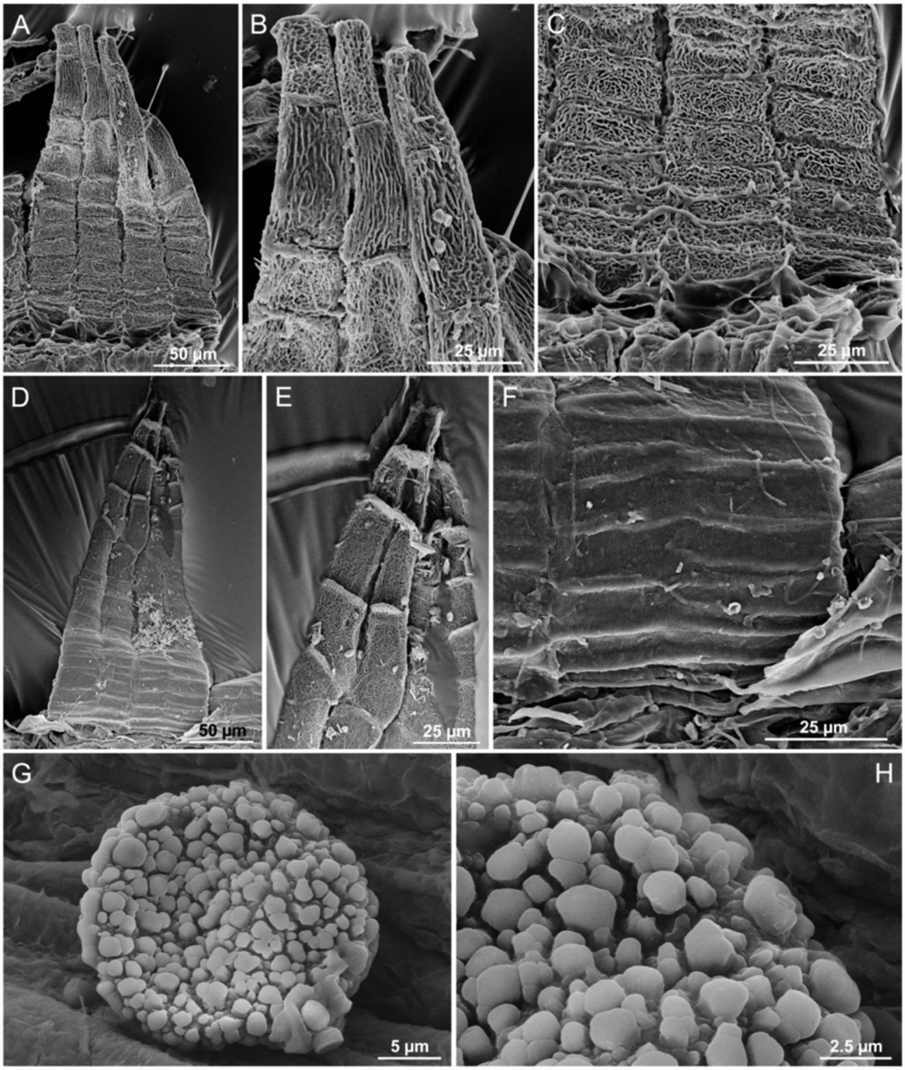


FIG. 61 – *Ulota ecklonii* (Hornsch.) A. Jaeger. A, outer surface of exostome; B, outer surface of upper exostome; C, outer surface of basal exostome; D, inner surface of exostome; E, inner surface of upper exostome; F, inner surface of basal exostome; G, a spore; H, surface ornamentation of a spore. (All from the isotype in S).

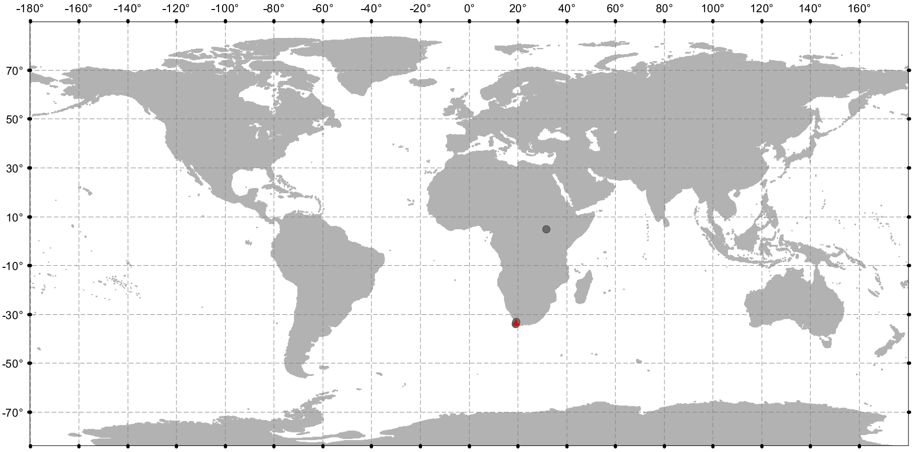


FIG. 62 – Distribution of *Ulota ecklonii* worldwide. The red triangle indicates the type locality.

Additional Specimens Examined: **South Africa**. WESTERN CAPE: Hottentots Holland, *C. Thorne 3638* (PRE), Table Mountain, *s.coll.* (S), *A. J. Hedderson 13365* (UBC).

South Sudan. JUBA: *J. Ch. Meylan s.n.* (H).

14. **ULOTA EURYSTOMA** Nog., J. Sci. Hiroshima Univ., Ser. B, Div. 2 (Bot.) 3: 213. 18 f. 1–10. 1939. TYPE: JAPAN. Honshu, Mt. Hirakura, 29 Mar. 1938, *R. Toyama 2650* (isotype, KYO!).

Plants ca. 1.5 cm tall, yellow to green on the top, brown to black below. Stems usually branched. Leaves strongly crisped when dry, patent when moist, (1.6–) 2.2–2.6 (–2.7) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded, concave; apex acuminate; leaf margin plane and irregularly partially recurved; costa strong, ending near the apex. Upper and middle laminal cells irregularly rounded, (5–) 8–12 (–16) × (6–) 8–9 (–12) μm, thick-walled, often with low simple papillae or nearly smooth; basal inner cells rhomboidal, rectangular to elongate-rectangular, (15–) 22–33 (–49) × (2–) 3–6 (–9) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in (3–) 4–8 (–11) rows hyaline band, quadrate to rectangular, with thickened transverse walls.

Autoicous. Perichaetial leaves hardly differentiated, (1.3–) 2.2–2.9 (–3) mm. Vaginula not seen. Seta ca. 4 mm long, slightly twisted anticlockwise when dry. Capsule short exserted, ca. 2.5 mm long. Urn obovoid or funnel-shaped, not or slightly constricted when dry and empty, eight furrows sometimes obscurely present and, if so, along the entire length. Neck short, abruptly or gradually narrowed to the seta. Exothecial cells indistinctly differentiated into eight bands, almost as long as an urn, two to three cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction of urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, variably incurved, erect or spreading, reflexed when dry, lanceolate, wrinkle throughout outside, striolate or nearly smooth inside. Endostome segments 8, linear, hyaline or pale yellow, almost reaching the exostome teeth, uniseriate, smooth on both sides, ventral trabeculae often distinct. Opercula not seen. Calyptra mitrate, sparsely to densely hairy. Spores irregularly shaped, finely papillose, all precociously germinated, we seen, 24–27 μm in diameter.

Illustration: Noguchi (1939) and Wang and Jia (2012a); figures 63–65.

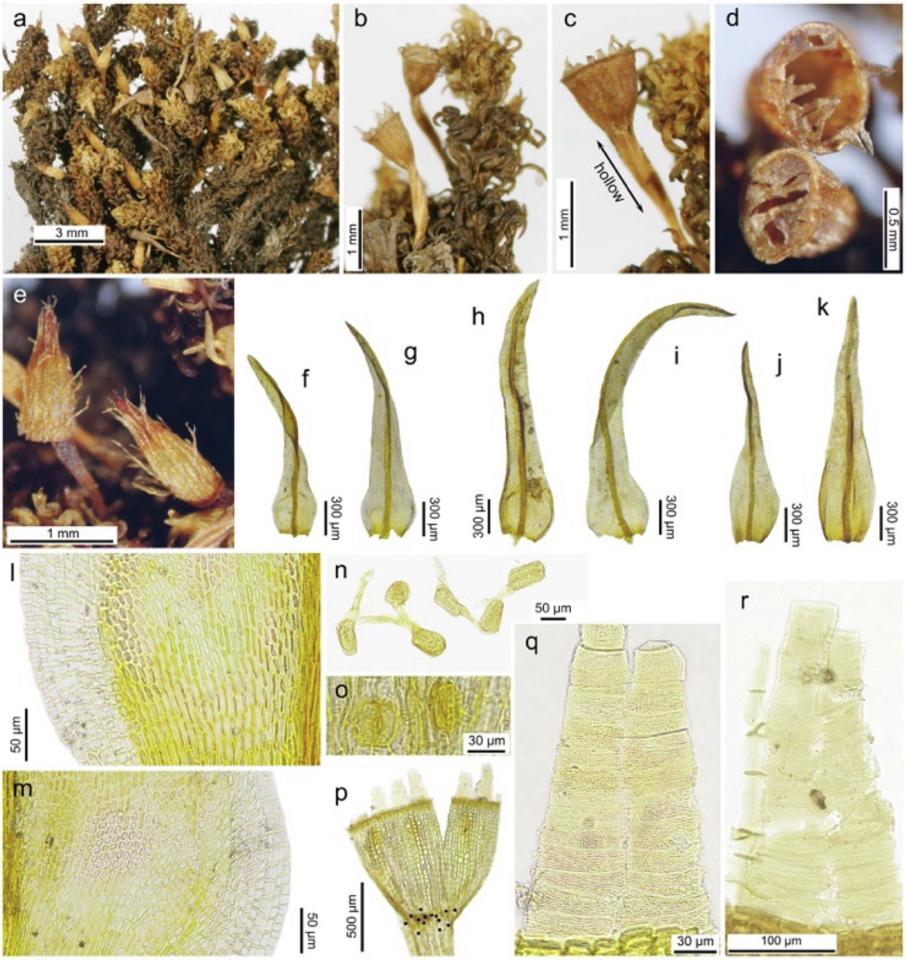


Fig. 63 – *Ulota eurystoma* Nog. a. Habit. b–c. Capsules in dry and empty. d. Capsule mouths viewed from above. e. Calyptra. f–i. Leaves. j–k. Inner perichaetial leaves. l–m. Marginal cells at leaf base. n. Germinated spores. o. Stomata. p. Exothecial wall, with dots indicating stoma position. q. Exostome teeth. r. Endostome segment. (All from the isotype in KYO, except n and r from *Nakanishi 86* [non-type, HYO], q from *Iwatsuki* [non-type, S]).

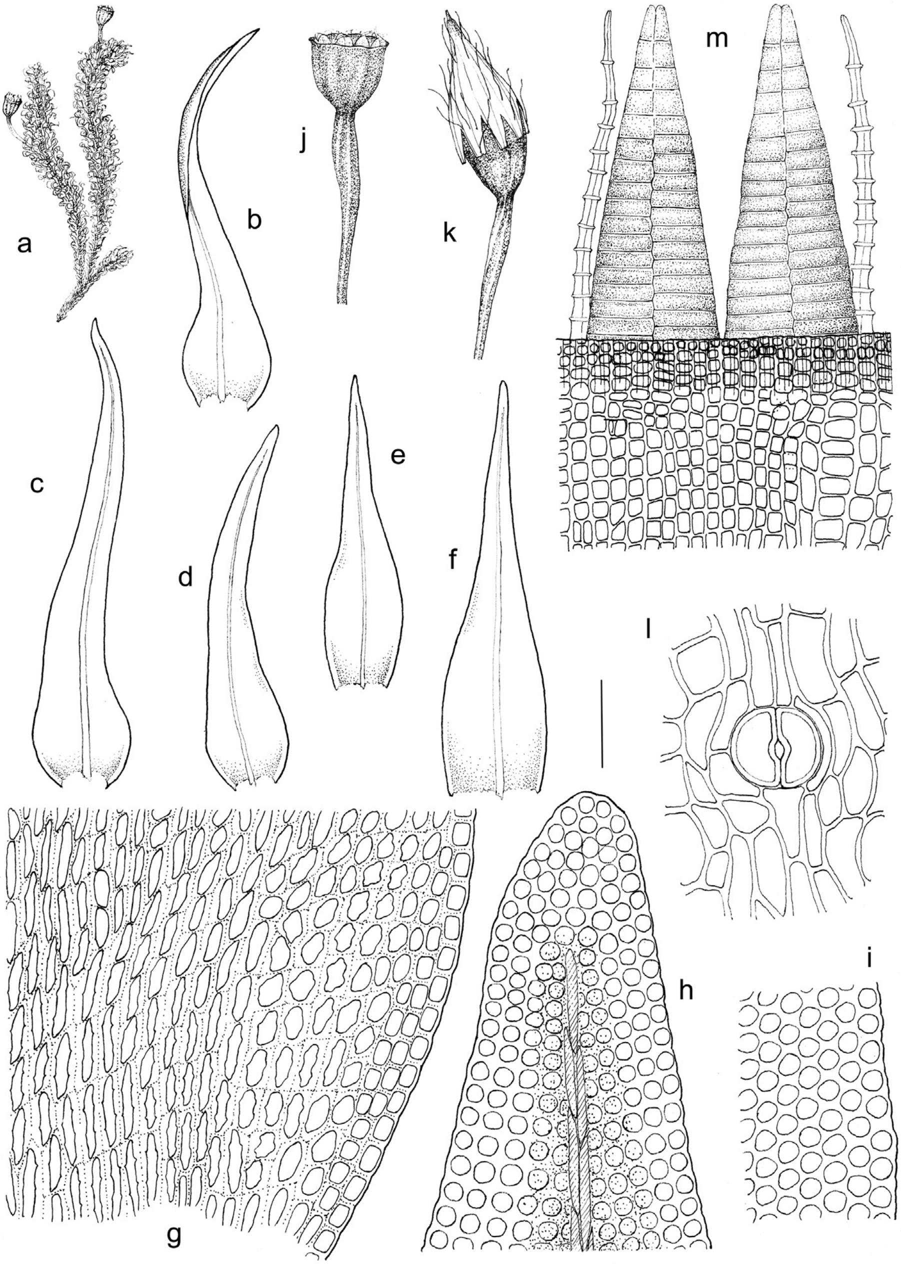


FIG. 64 – *Ulota eurystoma* Nog. a. plant; b–d. leaves; e–f. perichaetial leaves; g. basal marginal cells; h. top laminal cells; i. median marginal cells; j. an empty capsule in dry; k. a capsule with calyptra; l. stoma; m. a portion of peristome. (Scale bar: a, 4 mm; b–f, 0.48 mm; g–i and l, 0.04 mm; j–k, 0.95 mm; m, 0.1 mm. All drawn from isotype in KYO).

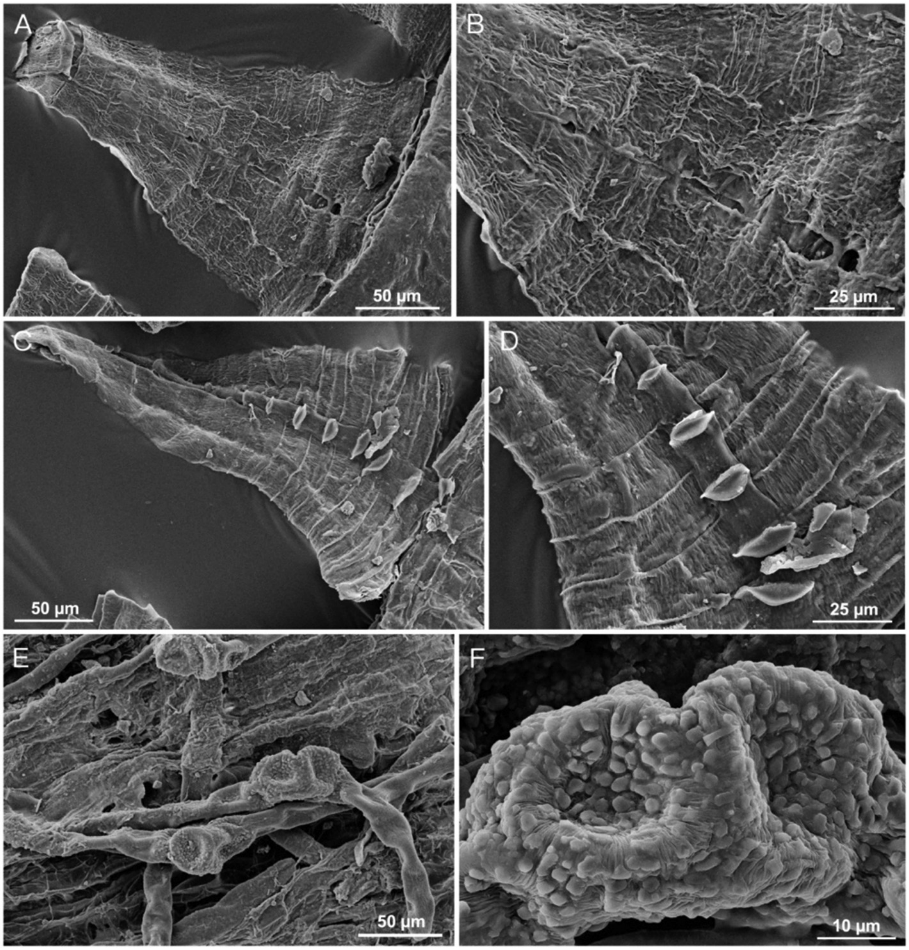


Fig. 65 – *Ulota eurystoma* Nog. A, outer surface of exostome; B, outer surface of middle exostome; C, inner surface of exostome and endostome; D, inner surface of basal exostome and endostome; E, germinated spores; F, surface ornamentation of a germinated spore. (All from the isotype in KYO).

Habitat: It grows on branches of trees, according to the only record. There are two records of altitude: 1400–1700 m.

Distribution: It is **endemic** to Japan. Figure 66.

Notes: *Ulota eurystoma* is a rare and unusual species, characteristic of obovoid or funnel-shaped capsules that are not constricted when dry and exostome teeth with very weak ornamentation.

Ulota eurystoma was described (Wang and Jia, 2012a) as having quite a long neck and a very short seta. Later, based on critical observation of more specimens, we found that the upper part of the seta tends to be hollow (figure 63c) and slightly thicker than the lower part, but it should still belong to the seta rather than the

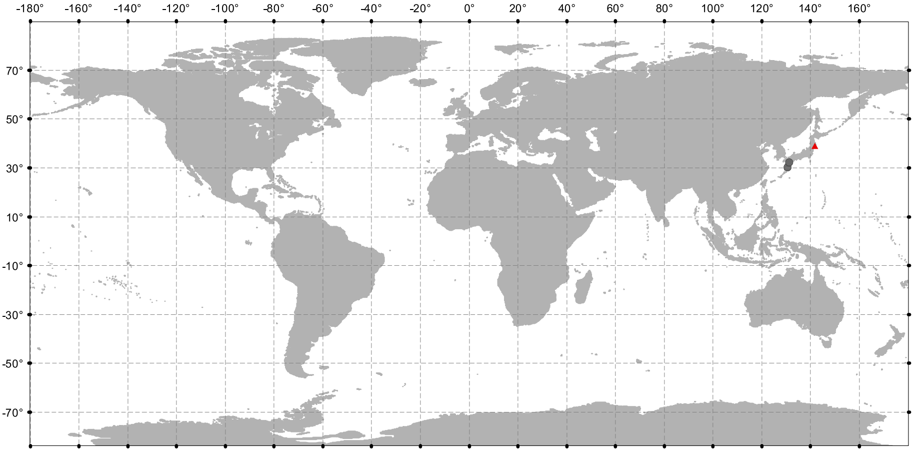


FIG. 66 – Distribution of *Ulota eurystoma* worldwide. The red triangle indicates the type locality.

neck. Therefore, this feature was described incorrectly before (Wang and Jia, 2012a), and a similar case was also found in *Ulota yakushimensis*. Additionally, the spores we have seen are not many, and all have precociously germinated, but the size is similar to that reported before (20–30 μm in Noguchi and Iwatsuki, 1989).

In *Ulota*, there are a few species whose capsules are hardly or weakly constricted when dry, and their mouth is the widest part of the whole capsules, which makes them more or less funnel-shaped. They are *Ulota eurystoma*, *U. obtusiuscula*, *U. rehmannii*, *U. reptans*, and *U. robusta*. All of them are endemic to Asia, except *Ulota obtusiuscula* from North America and *U. rehmannii* sporadically present in Eurasia. However, *Ulota obtusiuscula* can be distinguished from *U. eurystoma* by the large plants (2–2.5 cm), capsules often with long necks when dry and empty, quite a long seta (5–7.5 mm), strongly ornamentated exostome teeth and scabrous endostome segments; *U. rehmannii* by the flexuose leaves, strongly striolate exostome teeth, finely papillose endostome segments and nearly naked calyptra; *U. reptans* by the erect to flexuose leaves with small size (1.3–1.6 mm), weakly differentiated cells at basal leaf margins (≤3 rows), strongly ornamentated exostome teeth, often sparsely hairy calyptra and larger spores (30–38 μm); *U. robusta* by the flexuose to moderately crisped leaves, long seta (3–6 mm), wide endostome segments, strongly ornamentated exostome teeth and large spores (32–37 μm).

In the specimens we studied, *Ulota eurystoma* is often misidentified as the local *U. yakushimensis*. In both having leaves with a rounded base and acuminate apex, distinctly differentiated cells at basal leaf margins, capsules not or hardly constricted when dry and not cylindrical in shape, and seta usually becoming hollow and thicker in the upper part. But *Ulota yakushimensis* differs in flexuose leaves, capsules without the wide mouth, strongly ornamentated exostome teeth, absent endostome segments, and large multicellular spores (79–91 μm).

Although the exostome teeth in the type materials are mostly erect, those in non-type specimens examined in this study are mostly reflexed.

Key to *Ulota eurystoma* and its closely related species.

1. Endostome segments wide, lanceolate.. *U. robusta*
1. Endostome segments narrow, linear to narrow-lanceolate..............................2
2. Leaf cells at basal margins weakly differentiated, ≤3 rows................ *U. reptans*
2. Leaf cells at basal margins distinctly differentiated in 3–12 rows.....................3
3. Exostome teeth prominently variably striate outside; calyptra naked or sparsely hairy.. *U. rehmannii*
3. Exostome teeth papillose or slightly striate near the apex outside; calyptra densely hairy..4
4. Plants larger, 2–2.5 cm; capsules often with long neck when dry and empty; seta much longer, 5–7.5 mm; endostome segments slightly scabrous .... *U. obtusiuscula*
4. Plants relatively small, ca. 1.3 cm; capsules often with short neck; seta relatively short, 0.7–2.5 mm; endostome segments smooth or absent.................................5
5. Leaves often flexuose when dry; exostome teeth strongly ornamentated with densely papillose to papillose-striate; endostome segments absent; spores multicellular; capsule mouth slightly constricted and not the widest part when dry.. *U. yakushimensis*
5. Leaves strongly crisped when dry; exostome teeth weakly ornamentated with wrinkle to striolate; endostome segments well-developed and smooth; spores unicellular; capsule mouth not constricted and are the widest part when dry... *U. eurystoma*

Additional Specimens Examined: **Japan**. KAGOSHIMA: Isl. Yakushima, 5 Dec. 1964, *Z. Iwatsuki, A. J. & E. Sharp* (H, MICH, S), 25 Jul. 1962, *S. Nakanishi 86* (HYO). KUMAMOTO: summit of Mt. Ichifusa, alt. ca. 1700 m, 25 May 1955, *Z. Iwatsuki s.n.* (S).

15. **ULOTA FUEGIANA** Mitt., J. Proc. Linn. Soc., Bot. 4: 76. 1859. TYPE: CHILE. Tierra del Fuego, “Hermite island, Cape Horn”, 1839–1843, *J. D. Hooker 141b* (holotype, NY; isotypes, BM00919961! BM000976120! BM000873144! E00052653–54! PC0108132–33!).

Ulota angustissima Müll. Hal., Hedwigia 36: 104. 1897. ***syn. nov.*** TYPE: CHILE. Valdivia, 1888, *Dr. H. Hahn* (holotype, G; isotypes, S-B88536! NY).

Ulota carinata Mitt., J. Proc. Linn. Soc., Bot. 4: 75. 1859. ≡ *Orthotrichum carinatum* (Mitt.) Mitt., J. Linn. Soc., Bot. 12: 190. 1869. TYPE: CHILE. *Mr. Lobb 35* (holotype, NY; isotypes, MICH526538! BM000825444!). Proposed by Wang and Jia (2016).

Ulota eremitensis Mitt., J. Proc. Linn. Soc., Bot. 4: 76. 1859. ≡ *Orthotrichum eremitense* (Mitt.) Mitt., J. Linn. Soc., Bot. 12: 189. 1869. TYPE: CHILE. Tierra del Fuego, “Hermite Island, Cape Horn”, *J. D. Hooker s.n.* (holotype, NY).

Ulota fernandeziana Malta, Acta Horti Bot. Univ. Latv. 2: 202. f. 20. 1927. Type: Chile. Juan Fernandez: Masafuera, Cordon de Borril, an Drimys, 1 Mar. 1917, *C. et I. Skottsberg sub n.165* (holotype, H4334033! isotype, S-B127726!). Proposed by Wang and Jia (2016).

Ulota fuegiana subsp. *darwinii* (Mitt.) Malta, Acta Horti Bot. Univ. Latv. 2: 188. 1927. ≡ *Ulota darwinii* Mitt., J. Proc. Linn. Soc., Bot. 4: 77. 1859. Type: Argentina. Terra del Fuego, 1833, *C. Darwin* (holotype, NY; isotypes, BM, PC00100148!).

Ulota fuegiana var. *crispata* Malta, Acta Horti Bot. Univ. Latv. 2: 202. 1927. Type: Chile. Valdivia, 1888, *H. Hahn* (holotype, H4334032! isotype, S-B181068!). Proposed by Wang and Jia (2016).

Ulota glabella Mitt., J. Proc. Linn. Soc., Bot. 4: 76. 1859. Type: Chile. Tierra del Fuego, "Hermite island, Cape Horn", 1839–1843, *J. D. Hooker 141a* (holotype, NY; isotypes, BM000919960! E00052673! E00052655! PC0108133! PC0101534!). Proposed by Wang and Jia (2016).

Ulota hermitei Besch., Miss. Sci. Cape Horn, Bot. 5 (Bot.): 274. 1889. *illegitimate, type of earlier name included.* Type: Chile. Baie Orange (île Hoste) Terre de Feu, 25 Jul. 1883, *P. A. Hariot 150* (holotype, PC0703858–61!).

Ulota rufula var. *patagonica* Malta, Acta Horti Bot. Univ. Latv. 2: 200. f. 19: d–g. 1927. Type: Chile. "Río Aysen, in ramulis.", Jan. 1897, *P. Dusén 516* (holotype, H4334002! isotype, PC!). Proposed by Wang and Jia (2016).

Plants 0.5–1.5 (–2) cm tall, green above, gradually brown below. Stems usually branched. Leaves distinctly flexuose, sometimes variably crisped when dry, patent when moist, (1.3–) 1.8–2.4 (–2.8) mm long, leaf lamina lanceolate, unistratose; leaf base more or less wide, rounded; apex long acuminate; leaf margin plane or slightly partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, (4–) 7–10 (–15) × (4–) 7–9 (–12) μm, thick-walled, with 1–2 low simple papillae per cell, unbranched; basal inner cells linear, elongate-rectangular and vermicular, (18–) 28–41 (–54) × (1–) 2–3 (–4) μm, smooth, strongly thickened wall; basal marginal cells differentiated in (3–) 6–10 (–15) rows, hyaline, quadrate to rectangular, with only transversely thickened walls, sometimes with thin or equally slightly thickened walls.

Autoicous. Perichaetial leaves somewhat longer, (2–) 2.4–2.9 (–3.1) mm. Vaginula naked. Seta (2.2–) 3.2–4.5 (–6) mm long, twisted anticlockwise when dry. Capsules short to long exserted, 1.3–1.8 mm long. Urn cylindrical, slightly, sometimes strongly constricted when dry and empty, with eight ridges along the entire length. Neck short, abruptly narrowed to the seta. Exothecial cells clearly differentiated into eight bands. Stomata superficial, on the central part, sometimes on the lower part of the urn. Preperistome is rarely present. Peristome double. Exostome teeth 16, united into 8 pairs, recurved and lying on the exothecium when dry, lanceolate, densely papillose on both surfaces, rarely striate near the base. Endostome segments 8, filiform, fragile, almost as tall as the exostome, uniseriate, ca. 1/6 width of teeth in the middle, hyaline, smooth on the outside, slightly coarse on the inside. Opercula with a short to long beak. Calyptra mitrate, densely hairy, sometimes naked. Spores spherical, brownish, finely papillose, (23–) 26–30 (–38) μm in diameter.

Illustration: Malta (1927) and Wang and Jia (2016); figures 67 and 68.

Habitat: It grows on branches or trunks of trees, such as *Berberis*, *Desfontainia*, and *Nothofagus*. There are many records of altitude: 40–1055 (–1150) m.

Distribution: It is common in the southern part of Chile and Argentina. Figure 69.

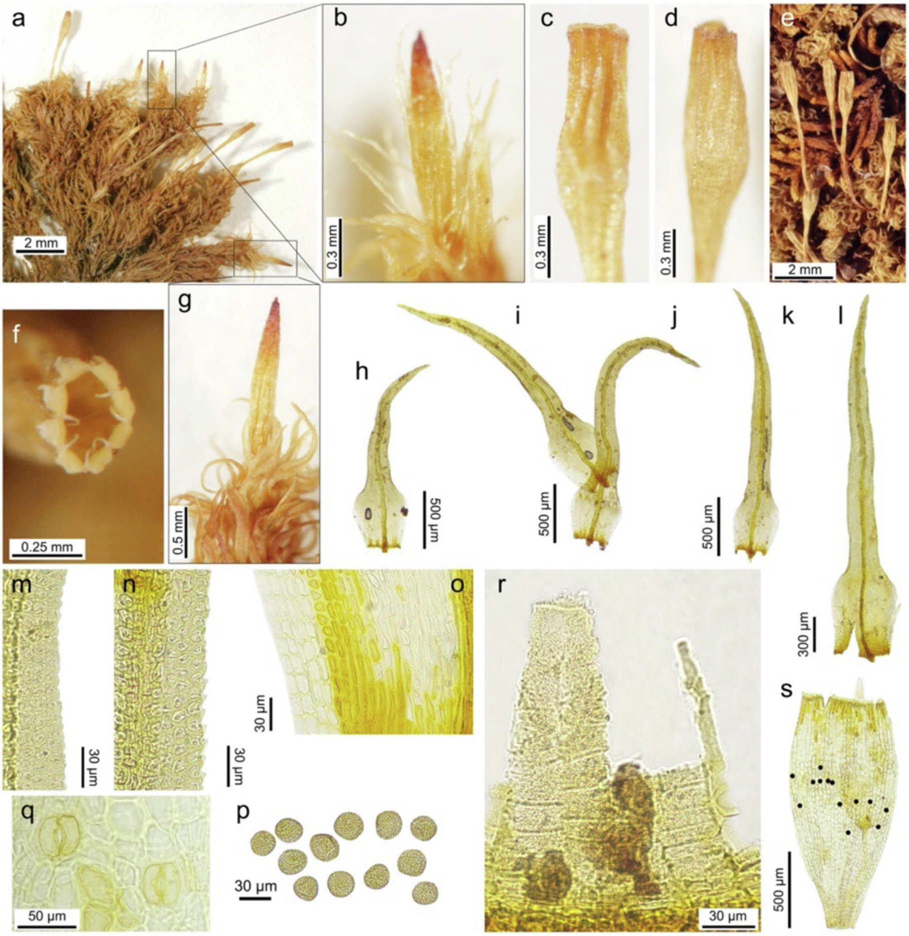


FIG. 67 – *Ulota fuegiana* Mitt. a and e. Habit. c–d. Capsules in dry and empty. b and g. Calyptra. f. Capsule mouth viewed from above. h–k. Leaves. l. Perichaetial leaf. m–n. Leaf marginal cells at upper part. o. Marginal cells at leaf base. p. Spores. q. Stomata. r. Incomplete peristome. s. Exothecial wall, with dots indicating stoma position. (All from the isotype in E, except e–f from *T. Seki s.n.* [non-type, H] and p from *J. F. Engel* [non-type, H]).

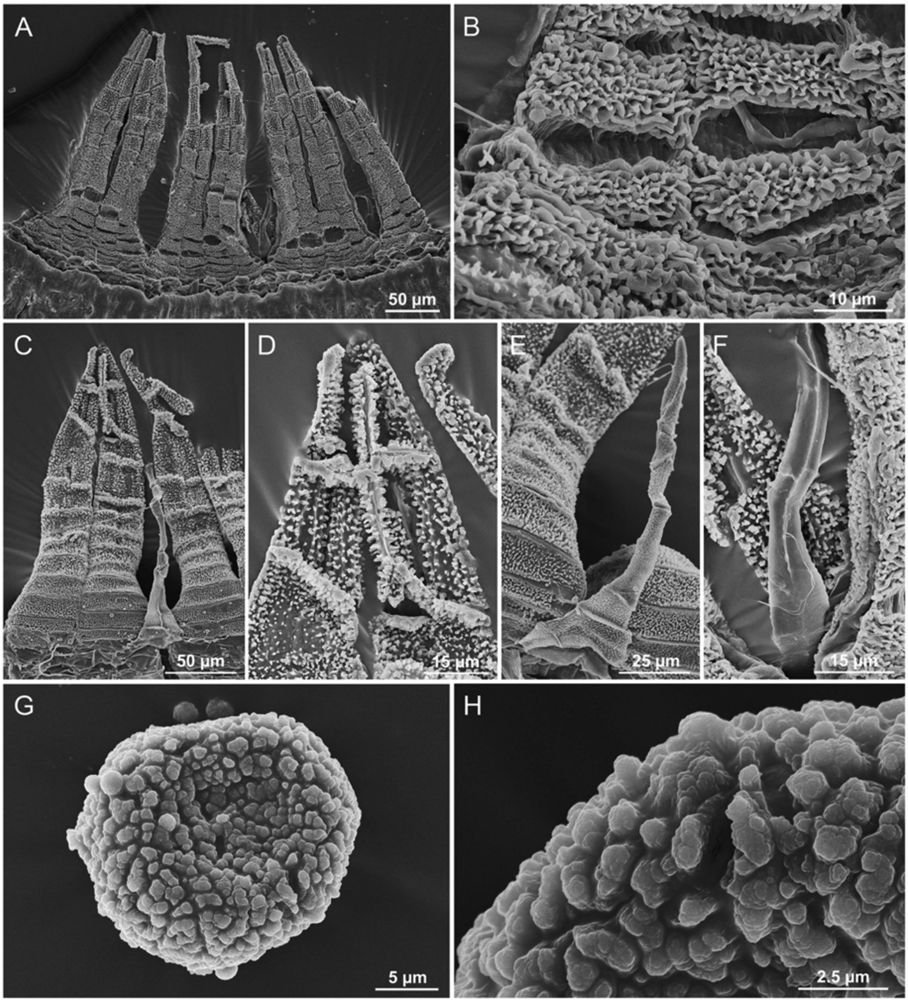


FIG. 68 – *Ulota fuegiana* Mitt. A, outer view of exostome; B, outer surface of basal exostome; C, inner view of exostome; D, inner surface of upper exostome; E, inner view of endostome; F, outer surface of endosotme; G, a spore; H, surface ornamentation of a spore. (All from *T. Seki s.n.* [non-type, H]).

Notes: The spirally twisted leaves of *Ulota angustissima* were considered by Müller as an important difference from other species in the genus in the protologue (1897), and Malta (1927) suggested that it probably belonged to *Macromitrium* Brid. However, after examining the scanty type materials from S (figure 70) and the photo of holotype from G (downloaded from Global Plants: https://plants.jstor.org), we found that it is quite similar to *U. fuegiana* in many features, including flexuose to twisted, crisped leaves, lanceolate with the long acuminate apex in leaf shape, 4–5 rows of hyaline cells at the basal leaf margin, cylindrical capsule, long seta and

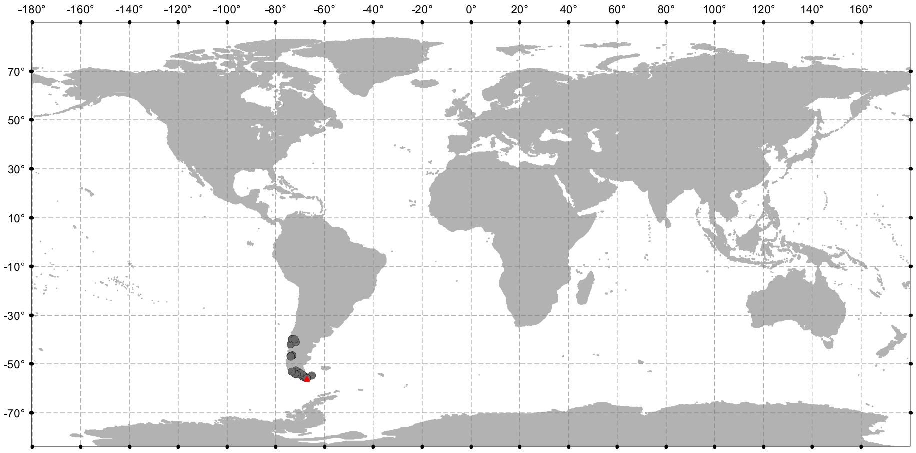


FIG. 69 – Distribution of *Ulota fuegiana* worldwide. The red triangle indicates the type locality.

stomata located at the urn. Therefore, we reduce it as a synonym of *U. fuegiana* here, although the endostome segments are missing in the isotype of S.

Recently, Garilleti *et al.* (2020) reinstated *Ulota glabella* and considered that it differs from *U. fuegiana* in the nakedness of the calyptra, the brown-orange to pale orange exostome teeth, the endostome segments with high papillose, the highly developed exostomial trabeculae and the crenulate leaf margin. But these differences are either absent or minor based on our examination, even between the type collections (figures 67 and 71), except for the nakedness of the calyptra. Moreover, the calyptra in *Ulota fuegiana* varies greatly in some cases, from naked to hairy, which is clearly shown even in the type materials (figure 67), although Garilleti *et al.* (2020) stated that they have never found it. In fact, there are some differences in leaf shape and thickness of hyaline cell walls at basal leaf margins between *Ulota fuegiana* and *U. glabella*. For example, in the type materials, *Ulota fuegiana* has wide leaf bases and hyaline cells at basal leaf margins with only transversely thickened walls, while *U. glabella* has narrow leaf bases and hyaline cells at basal leaf margins with thin or equally slightly thickened walls. But there is no regular pattern between these two characters. For instance, *Ulota hermitei* (figure 72), as a synonym of *U. glabella* (Malta, 1927), has hyaline cells at basal leaf margins with thin or equally slightly thickened walls but wide leaf bases. The opposite case exists in *Ulota angustissima* (figure 70). Certainly, similar variations also appeared in some non-type specimens during our study (figure 73). Therefore, we insist on regarding *Ulota glabella* as a synonym of *U. fuegiana* before seeing the specimens used by Garilleti *et al.* (2020).

The main diagnostic characteristics of *Ulota fuegiana* are the flexuose or slightly crisped leaves, markedly differentiated basal marginal leaf cells, stomata restricted to the urn, eight filiform, fragile endostome segments, and often hairy calyptra.

Ulota fuegiana is very similar to the local *U. germana*, and the latter differs in the strongly crisped leaves, the longer perichaetial leaves (2.8–3.4 mm), distinctly

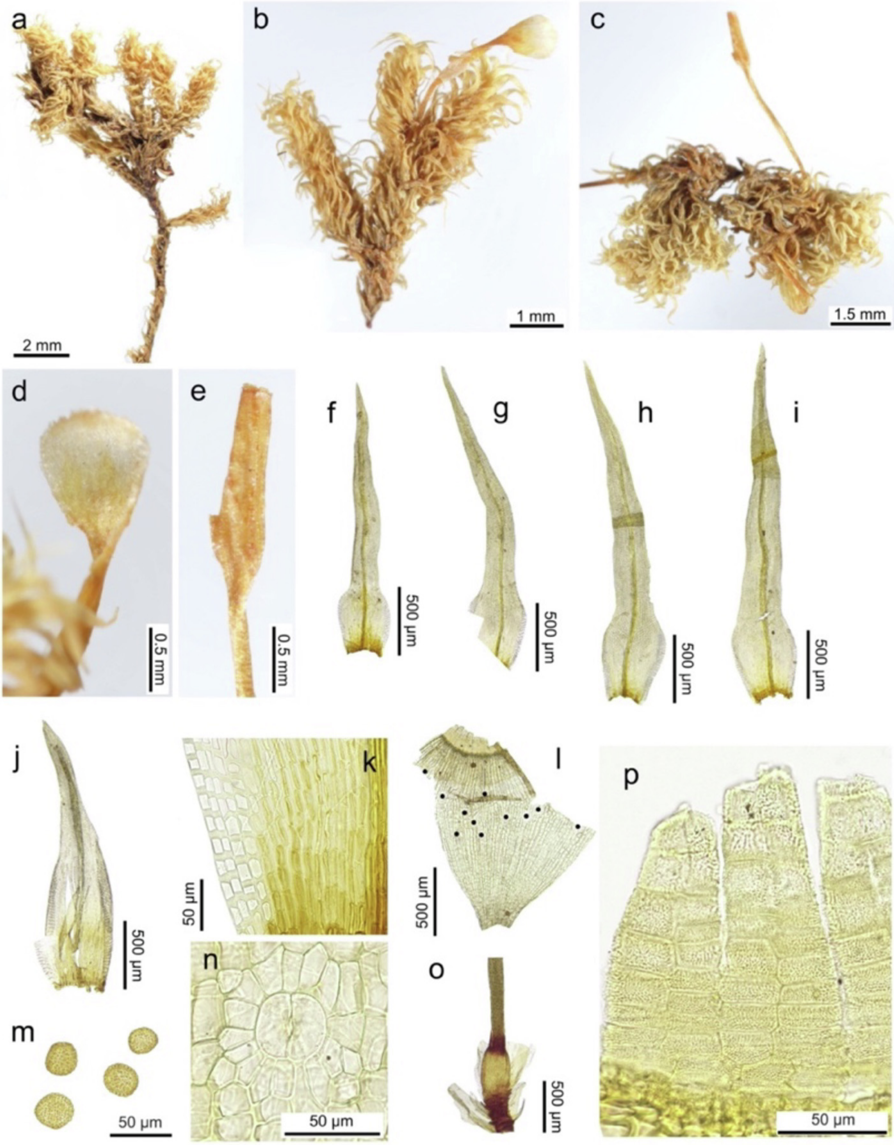


FIG. 70 – *Ulota angustissima* Müll. Hal. a–c. Habit. d–e. Broken capsules in dry and empty. f–i. Leaves. j. Inner perichaetial leaf. k. Marginal cells at leaf base. l. Exothecial wall, with dots indicating stoma position. m. Spores. n. Stoma. o. Vaginula. p. Peristome, with endostome segments all fallen. (All from the isotype in S).

constricted capsules, shorter seta (1.7–2.9 mm), narrow-lanceolate endostome segments (neither filiform nor fragile) and stomata located at the lower part of urn or the junction between urn and neck. *Ulota fuegiana* also resembles the Australian

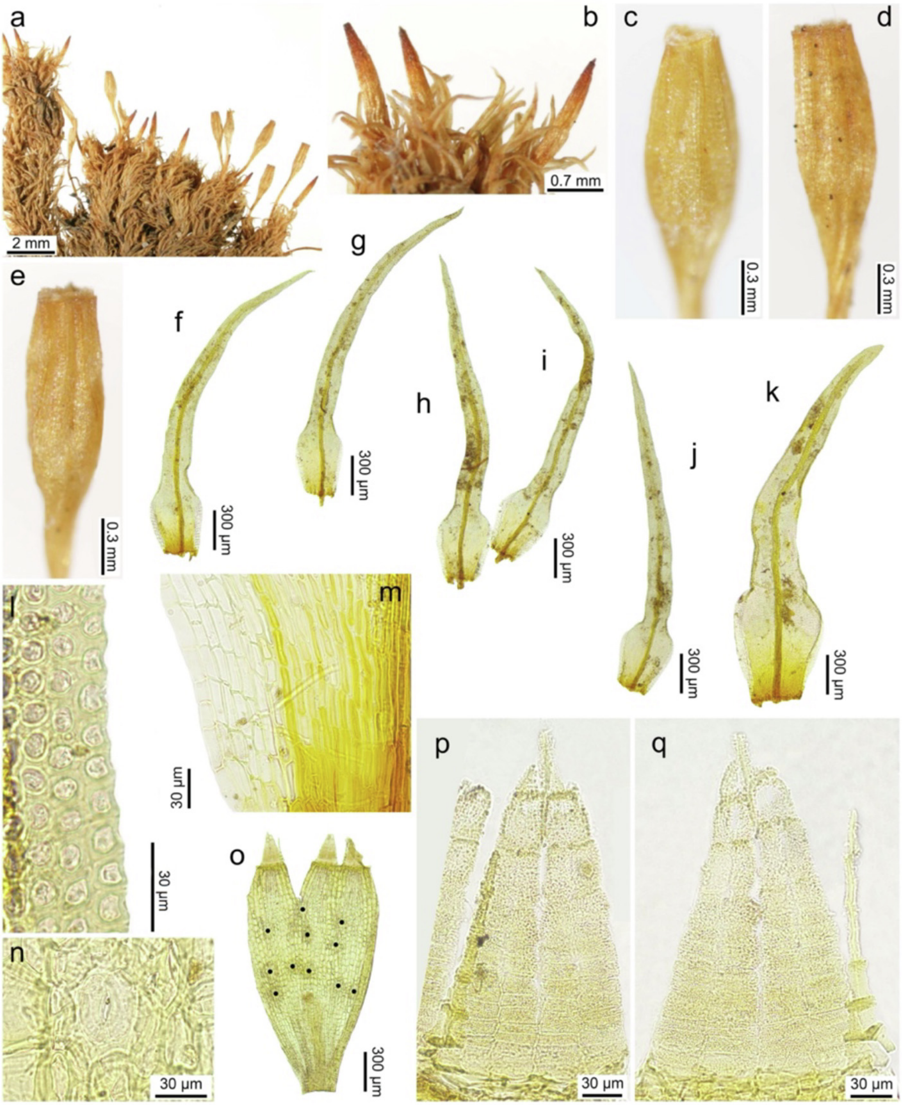


FIG. 71 – *Ulota glabella* Mitt. a. Habit. b. Calyptra. c–e. Capsules in dry and empty. f–j. Leaves. k. Perichaetial leaf. l. Leaf marginal cells at upper part. m. Marginal cells at leaf base. n. Stoma. o. Exothecial wall, with dots indicating stoma position. p–q. Peristome. (All from the isotype in E).

U. cochleata. Both share in the filiform endostome segments and stomata on the central part of the urn. However, *Ulota cochleata* is distinguished by the strongly crisped leaves and less rows (4–7) of hyaline cells at the leaf marginal base.

As mentioned above, there are some variations in leaf shape, the thickness of hyaline cell walls at basal leaf margins, and calyptra hairiness.

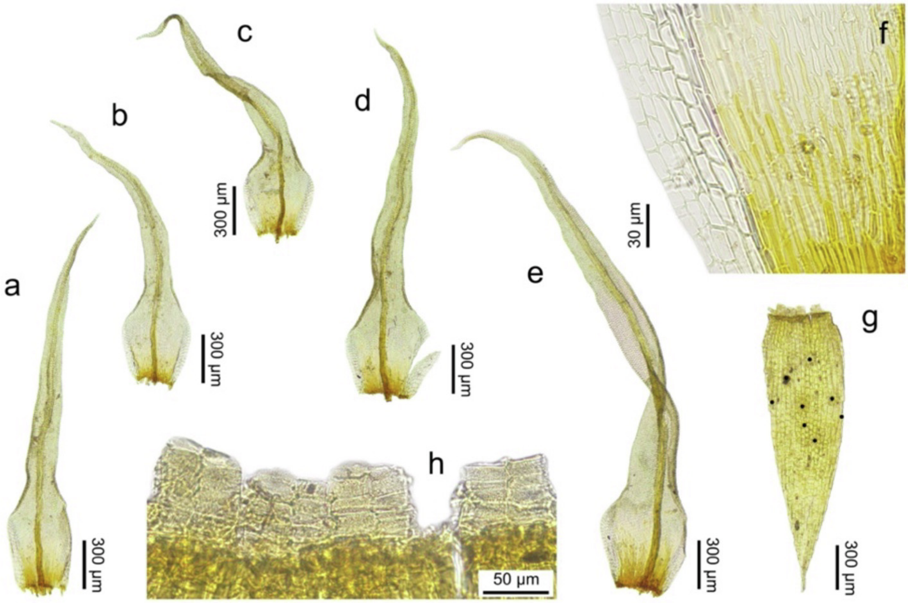


Fig. 72 – *Ulota hermitei* Besch. a–d. Leaves. e. Perichaetial leaf. f. Marginal cells at leaf base. g. Exothecial wall, with dots indicating stoma position. h. Broken peristome. (All from the holotype in PC).

Key to *Ulota fuegiana* and its closely related species.

1. Capsules always strongly constricted when dry; seta shorter, 1.7–2.9 mm; stomata on the lower part of urn or the junction between urn and neck; endostome segments linear to narrow-lanceolate, not fragile............................... *U. germana*
1. Capsules often slightly constricted when dry; seta longer, 3.2–5.5 mm; stomata often confined to the central part of urn; endostome segments often filiform, fragile...2
2. Leaves strongly twisted or crisped when dry; marginal cells at leaf base differentiated in less rows (4–7).. *U. cochleata*
2. Leaves usually flexuose when dry; marginal cells at leaf base differentiated in more rows (6–10)... *U. fuegiana*

Additional Specimens Examined: **Argentina**. Río Negro: Puerto Blest, 7 Jul. 1897, *P. Dusén 830* (S). Tierra del Fuego: Ushuaia, 17 Jan. 1986, *Matter 3455a* (MO, S).

Chile. Aysén: Estancia Río Circo, 3 Mar. 1967, *T. Seki 3/2-20* (H); San Rafael, Feb. 1921, *M. Gusinde s.n.* (S); Ventisquero San Rafael, 5 Mar. 1967, *T. Seki s.n.* (H); s. loc., 4 Feb. 1897, *P. Dusén 516* (PC). Los Lagos: Chiloé Island, 11 Mar. 1932, *Carl O. Enla.son 126* (MICH). Los Ríos: Valdivia, *W. Lechler s.n.* (PC), Oct. 1850, *527* (PC). Magallanes and Antártica: Fjardo Martinez, Bahia Plüschow, 21 Feb.

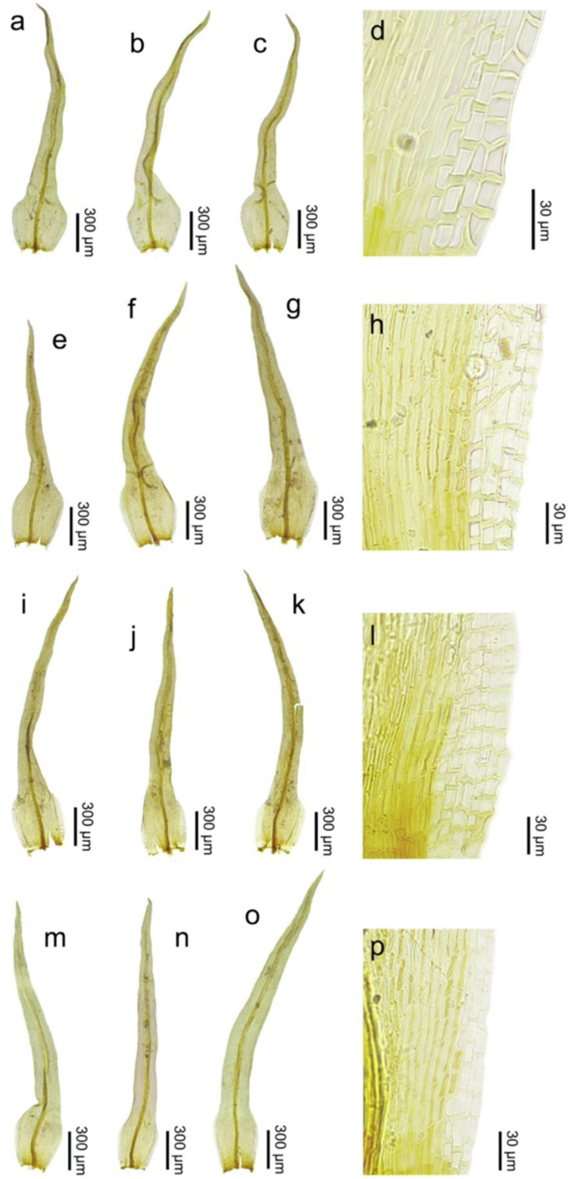


FIG. 73 – Leaf variations in *Ulota fuegiana* Mitt. a–c, e–g, i–k and m–o. Leaves. d, h, l and p. Marginal cells at leaf base. (a–d from *P. Dusén 830* [non-type, S], e–h from *T. Seki s.n.* [non-type, H], i–l from *M. Gusinde s.n.* [non-type, S], m–p from *J. D. Hooker s.n.* [non-type, H]).

1929, *H. Roivainen s.n.* (H); île Dawson, 19 May 1883, *J. H.* (PC), 25 Feb. 1908, *C. Skottsberg 451* (PC); Port Angosto, Dec. 1868, *Cunningham 160* (BM); Port Barrow, 4 Mar. 1909, *C. Skottsberg 450* (PC); Port Famine, 1890, *Marivault s.n.* (PC);

Port Gallant, *Cunningham s.n.* (MICH), 1867, *156* (H, MICH, PC0167429, PC0167446), *253* (BM & H); Port Selleert, 1867, *Cunningham 263* (PC); Puerto Tempanos, 17 Jun. 1908, *C. Skottsberg 457* (BM, PC & S); s. loc., *G. Renny s.n.* (PC); Skyring, 22 Apr. 1908, *T. Halle & C. Skottsberg 452* (PC); Puerto Cutter, *J. F. Engel s.n.* (H); Rio Azopardo, 27 Feb. 1896, *P. Dusén 264* (H, S); Tierre del Fuego, île Burnt, *J. H.* (PC), 1883, *O. Haney* (PC), *Hariot s.n.* (PC); île Hoste, Baie Orange, Aug. 1883, *O. Hanes s.n.* (PC), *J. H.* (PC), Baie Bokenika, 6 Nov. 1902, *C. Skottsberg 90* (PC), 1883, *Hariot s.n.* (PC167435, PC167437).

16. **Ulota germana** (Mont.) Mitt., J. Proc. Linn. Soc., Bot. 4: 76. 1859. ≡ *Orthotrichum germanum* Mont., Ann. Sci. Nat.; Bot., sér. 3 4: 121. 1845. Type: Chile. “in corticibus arborum reipublicae chilensis a cl. *Claude Gay.* lectum” (lectotype, PC0094403! designated by Garilleti *et al.*, 2020; isolectotypes, BM000873134–35! PC0100700–01! PC0108137!).

Ulota brevicollis (Mitt.) A.Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 164. 1874. ≡ *Orthotrichum brevicolle* Mitt., J. Linn. Soc., Bot. 12: 192. 1869. Type: Chile. prope urbem Valdivia, 1850, *W. Lechler 527* ex parte (holotype, NY; isotypes, S-B172018! PC0099361!). Proposed by Malta (1927) as a synonym of *U. rufula.*

Ulota chilensis (Mitt.) A.Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 164. 1874. ≡ *Orthotrichum chilense* Mitt., J. Linn. Soc., Bot. 12: 193. 1869. Type: Chile. prope urbem Valdivia, 1850, *W. Lechler 527* (holotype, NY; isotype, PC!). Proposed by Malta (1927) as a synonym of *U. rufula.*

Ulota lobbiana Mitt., J. Proc. Linn. Soc., Bot. 75. 1859. ≡ *Orthotrichum lobbianum* (Mitt.) Mitt., J. Linn. Soc., Bot. 12: 192. 1869. Type: Chile. Patagonia, *Mr. Lobb 35b* (holotype, NY; isotypes, BM000825445! MICH526540!). Proposed by Wang and Jia (2016).

Ulota persubulata Dusén, Rep. Princeton Univ. Exp. Patagonia, Botany 8(3): 122. 1903. *invalid, no description.* Type: Argentina. Nahuelhuapi (= Nahuel Huapi National Park) in truncis arborum, 7 Jul. 1897, *P. Dusén 791* (lectotype, S-B181245! designated by Wang and Jia, 2016; isolectotypes, BM000879989–90! H4334001! PC! S-B181246–47!). Proposed by Malta (1927) as a synonym of *U. rufula.*

Ulota rufula (Mitt.) A.Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 164. 1874. ≡ *Orthotrichum rufulum* Mitt., J. Linn. Soc., Bot. 12: 191. 1869. Type: Chile. prope urbem Valdivia, 1850, *W. Lechler 527,* ex parte (holotype, NY; isotypes, S! PC0099347!). Proposed by Wang and Jia (2016).

Ulota rufula var. *fagicola* Dusén ex Malta, Acta Horti Bot. Univ. Latv. 2: 200. f. 19: a–c. 1927. Type: Chile. in monte “Cordillera de la Costa” supra Angol app., in truncis arborm, 4 Nov. 1896, *P. Dusén 346a* (holotype, H4334023! isotype, S-B181242!). Proposed by Wang and Jia (2016).

Plants 0.5–2 cm tall, green above, brown to black below. Stems usually branched. Leaves strongly crisped, sometimes flexuose when dry, erect-spreading to patent when moist, (1.1–) 1.6–2.6 (–2.9) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex long acuminate; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, oblong, (7–) 10–12 (–15) × (6–) 7–9 (–11) μm, thick-walled, with 1 or 2 low papillae per cell; basal inner cells linear, elongate-rectangular, vermicular, (22–) 28–38 (–50) × (3–) 4–5 (–7) μm, with thick wall, smooth; basal marginal cells often differentiated in (4–) 6–10 (–15) rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves much longer, (2.5–) 2.8–3.4 mm, often sheathing the seta. Vaginula naked. Seta (1.2–) 1.7–2.9 (–4) mm. Capsules short to long exserted, 1–1.2 mm long, cylindrical when moist, strongly constricted when dry and empty, eight furrows along the entire length. Neck short, abruptly narrowed into seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, about four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the lower part of the urn or the junction between the urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, usually united into 8 pairs, lanceolate, densely papillose thorough or striate-papillose above on the outside, finely papillose thorough or striate at the base on the inside, revolute when dry, often lying on the exothecium when dry. Endostome segments 8, linear or narrow lanceolate, uniseriate, often 1/4 width of teeth in the middle part, almost as long as teeth, yellowish or hyaline, smooth on the outside, finely papillose to almost smooth on the inside. Opercula with a short beak. Calyptra mitrate, with densely long hairs. Spores spherical, finely papillose, (26–) 32–35 (–38) μm in diameter.

Illustration: Wang and Jia (2016); figures 74 and 75.

Habitat: It grows on branches and trunks of trees and shrubs, such as *Nothofagus* and *Gevuina*. There are some records of altitude: (60–) 557–1064 (–1150) m.

Distribution: It occurs in the southern part of Chile and Argentina and also disjunctively distributes in New Zealand (Wang and Jia, 2018a). Figure 76.

Notes: *Ulota germana* is recognized based on a unique combination of characters, including strongly crisped leaves, many rows of hyaline cells at basal leaf margins, much longer perichaetial leaves that often prominently sheathing around the seta, stomata located at the lower part of urn or the junction between urn and neck, eight narrow endostome segments and densely hairy calyptra.

Ulota germana resembles *U. fuegiana* in the conspicuously differentiated basal marginal leaf cells, eight endostome segments, and hairy calyptra. But *Ulota fuegiana* differs in usually having flexuose leaves, slightly constricted capsules, stomata restricted to the central part of the urn, shorter perichaetial leaves (2.4–2.9 mm), longer seta (3.2–4.5 mm) and filiform fragile endostome segments.

Besides that, *Ulota germana* also shares many characteristics with *U. crispa*, including strongly crisped leaves, conspicuously differentiated basal marginal leaf cells, often strongly constricted capsules, stomata located at the basal part of capsules, eight narrow endostome segments, and densely hairy calyptra. However, *Ulota crispa* is distinguished by the longer seta (3–5 mm), shorter perichaetial leaves (1.8–2.9 mm), longer capsules (1.4–2.2 mm), and smaller spores (19–25 μm).

The position of stomata varies little; some of them rarely appear in the central part of the urn, such as in the specimen *P. Dusén* (S-B157880).

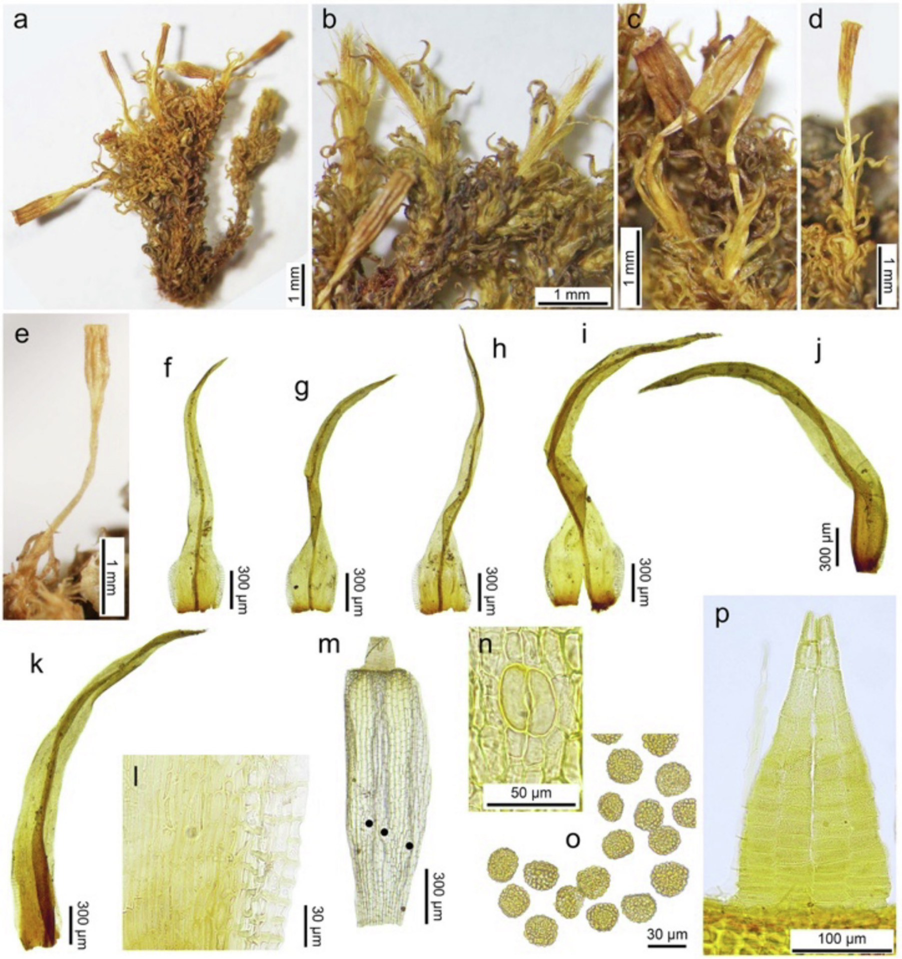


FIG. 74 – *Ulota germana* (Mont.) Mitt. a–b. Habit. c–e. Capsules in dry and empty. f–h. Leaves. i–k. Perichaetial leaves. l. Marginal cells at leaf base. m. Exothecial wall, with dots indicating stoma position. n. Stoma. o. Spores. p. Peristome. (a–d from the lectotype of *U. persubulata* [S-B181245], e–l from *T. Seki 2/32-61* [non-type, H3151091], m and o from and k and l from *R. R. Ireland & G. Bellolio 33500* [non-type, MO], n and p from *T. Seki 2/32-61* [non-type, H3151092]).

Key to *Ulota germana* and its closely related species.

1. Leaves usually flexuose when dry; capsules often slightly constricted when dry; stomata often confined to the central part of urn; endostome segments filiform, fragile..*U. fuegiana*
1. Leaves strongly crisped when dry; capsules always strongly constricted when dry; stomata on the lower part of urn or the junction between urn and neck; endostome segments linear to narrow-lanceolate, not fragile..........................2

2. Perichaetial leaves shorter, 1.8–2.9 mm, not prominently sheathing the seta; seta longer, 3–5 mm; capsules longer, 1.4–2.2 mm; spores relatively smaller, 19–25 μm..*U. crispa*
2. Perichaetial leaves longer, 2.8–3.4 mm, often prominently sheathing the seta; seta shorter, 1.7–2.9 mm; capsules shorter, 1–1.2 mm; spores large, 32–35 μm...*U. germana*

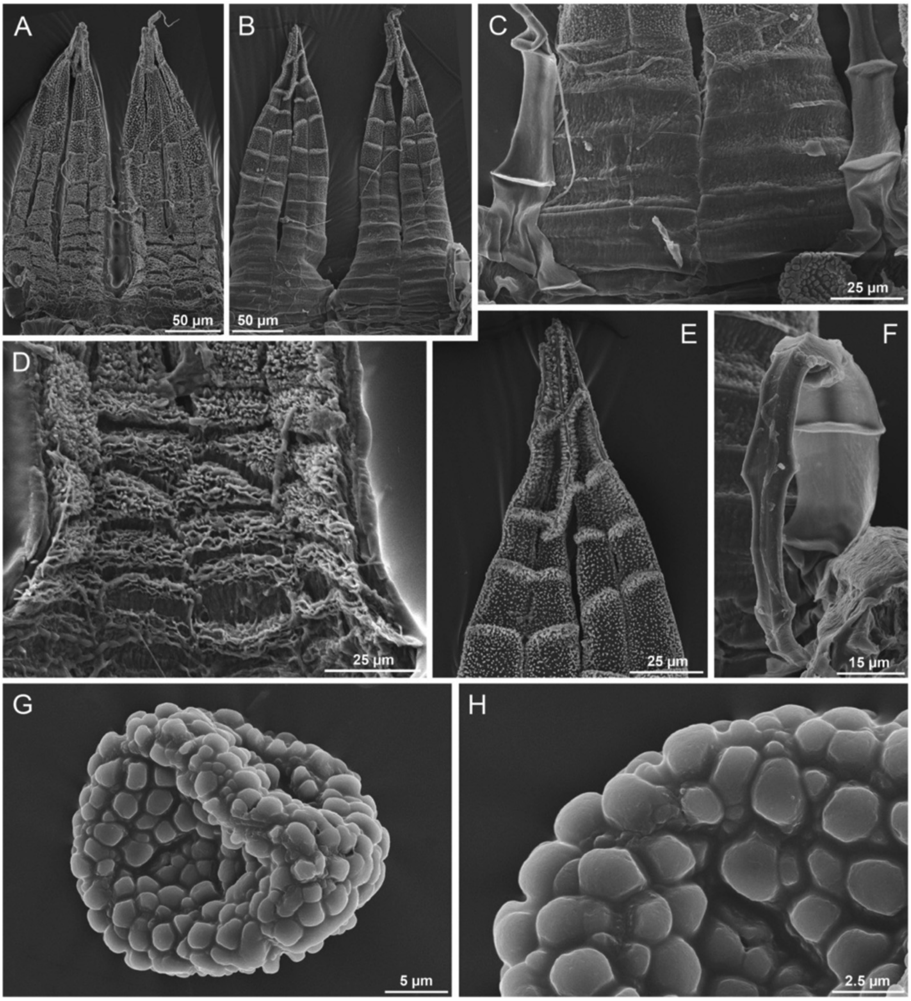


FIG. 75 – *Ulota germana* (Mont.) Mitt. A, outer surface of exostome; B, inner surface of exostome; C, inner surface of basal exostome and endostome; D, outer surface of basal exostome; E, inner surface of upper exostome; F, outer and inner surface of endostome; G, a spore; H, surface ornamentation of a spore. (All from *T. Seki no.2/32-61* [non-type, H3151091]).

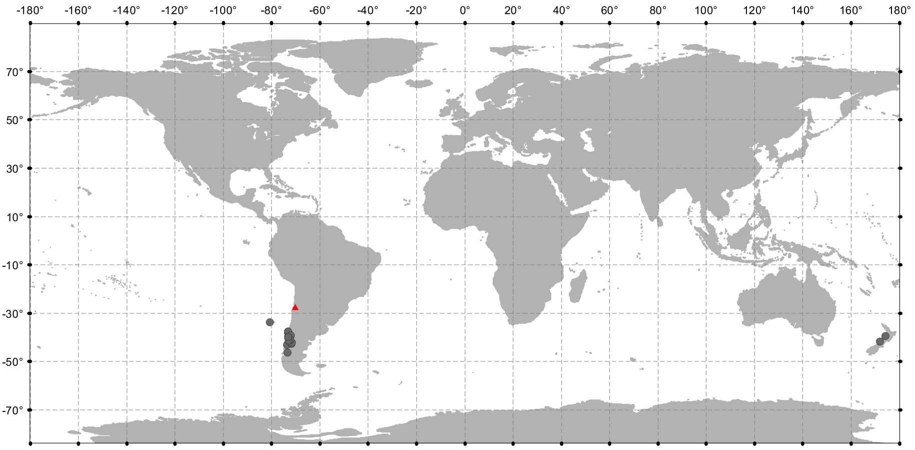


Fig. 76 – Distribution of *Ulota germana* worldwide. The red triangle indicates the type locality.

Additional Specimens Examined: **Argentina**. Chubut: Lago Menéndez, 21 Jan. 1938, *A. Kalela B248j(3)* (H).

Chile. Aysén: Río Exploradores, *T. Seki 2/32-61* (H); San Rafael, Feb. 1921, *M. Gusinde s.n.* (S). Bío Bío: Arauco, San Alfonso Farm, 29 Oct. 2001, *R. R. Ireland & G. Bellolio 32961* (BM, MO), 13 Nov. 2001, *33745* (MO). Los Lagos: Chiloé island, 7 Feb. 1976, M. R. Crosby 2548b (MO); Llanquihue, Rio Puelo, 4 Feb. 1948, *B. Sparre 4318* (S). Los Ríos: Valdivia, 1888, *H. Hahn s.n.* (H, S). Valparaíso: Masafuera, 25 Jan. 1955, *C. Skottsberg M124(1)* (S).

New Zealand. Nelson: Denniston, near parking area at top of Denniston Incline, alt. 580 m, 41°44′ S, 171°48′ E, 29 Nov. 1997, *Fife 11134* (CHR). Taranaki: Mt. Egmont, Sep. 1946, *W. Martin s.n.* (CHR).

17. **Ulota gigantospora** F. Lara, Caparrós & Garilleti, J. Bryology 33: 214. 2011. Type: China. Sichuan Prov., Jiulong County, mountain tributary of Wuxuhai-Jiulong valley below pass above Shandaoqiao village, SW of Jiulong, 28°58′6.6″ N, 101°24′1.9″ E, alt. ca. 4200 m; mossy *Abies/Rhododendron* forest along small stream; on *Abies* trunk, 17 Sep. 2010, *D. G. Long 40246*, (holotype, E00397912!).

Plants 1–2.6 cm tall, yellow to green above, brown to black below. Stems usually branched. Leaves variably crisped, sometimes flexuose when dry, erect-patent to patent when moist, (0.9–) 1.1–1.7 (–2.1) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex acuminate; leaf margin plane or slightly partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (7–) 9–11 (–14) × (6–) 7–9 (–11) μm, thick-walled, with low simple papillae, rarely branched; basal inner cells linear, elongate-rectangular to vermicular, (17–) 21–27 (–36) × (3–) 4–5 (–7) μm, with strongly thickened wall, smooth; basal marginal cells weakly differentiated, only 1–2 rows, hyaline, quadrate to rectangular, with only transverse walls often thickened.

Autoicous. Perichaetial leaves much longer, (1.6–) 1.7–2.6 (–2.8) mm. Vaginula often moderately hairy. Seta (3–) 3.3–4.8 (–5.2) mm long, twisted when dry. Capsule long exserted, 1.1–1.8 mm long. Urn short-cylindrical when empty and dry, subglobose when mature, slightly to strongly constricted below the mouth when dry and empty, eight furrows along the entire length, with prominent ribs alternately. Neck short to long, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, usually four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the transition zone between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, often recurved when dry and lying on the exothecium, lanceolate, densely and finely papillose on both sides, sometimes papillose-striate above on the outside, often more roughly, cancellate and with distinct trabeculae near the apex. Endostome segments 8, linear, almost as tall as teeth, bi- or uniseriate, hyaline, smooth on the outside, scabrous or obscurely papillose on the inside. Opercula with a long moderate beak. Calyptra mitrate, moderately hairy, occasionally sparsely hairy. Spores spherical, finely papillose, multicellular, large, (59–) 87–105 (–121) μm in diameter.

Illustration: Caparrós *et al.* (2011); figures 77 and 78.

Habitat: It grows on branches or trunks of trees, such as *Abies*. There are a few records of altitude: 3500–3750 m.

Distribution: It is **endemic** to China. Figure 79.

Notes: *Ulota gigantospora* is characterized by the combination of multicellular spores, weakly differentiated basal marginal leaf cells, short-cylindrical capsules, and double peristome.

The species with multicellular spores were once only three in *Ulota*, but recently there were five more reported (Garilleti *et al.*, 2012, 2015; Caparrós *et al.*, 2011). Besides *Ulota gigantospora*, they also include Australasian *U. membranata*, Asian *U. yunnanensis*, *U. novo-guinensis*, *U. yakushimensis* and South American *U. billbuckii, U. larrainii* and *U. streptodon. Ulota streptodon* can be distinguished from *U. gigantospora* by the non-crisped leaves, capsules with a somewhat puckered mouth, absent endostome segments, and urn-located stomata. *Ulota yakushimensis* differs in the non-crisped leaves, somewhat differentiated cells (3–6 rows) at basal leaf margins, short capsules that hardly constricted when dry, and absent endostome segments. *Ulota billbuckii, U. larrainii*, *U. membranata* and *U. novo-guinensis* are all distinct in 16 endostome segments, and the former two species are further different in flexuose leaves, and broad endostome segments *U. membranata* further in erect to flexuose leaves, somewhat differentiated cells (4–6 rows) at basal leaf margins and obovate or ovate-cylindrical capsules; *U. novo-guinensis* further in ovate leaf base and smooth endostome segments. *Ulota gigantospora* is mostly close to *U. yunnanensis*, and both additionally have crisped leaves, weakly differentiated cells at basal

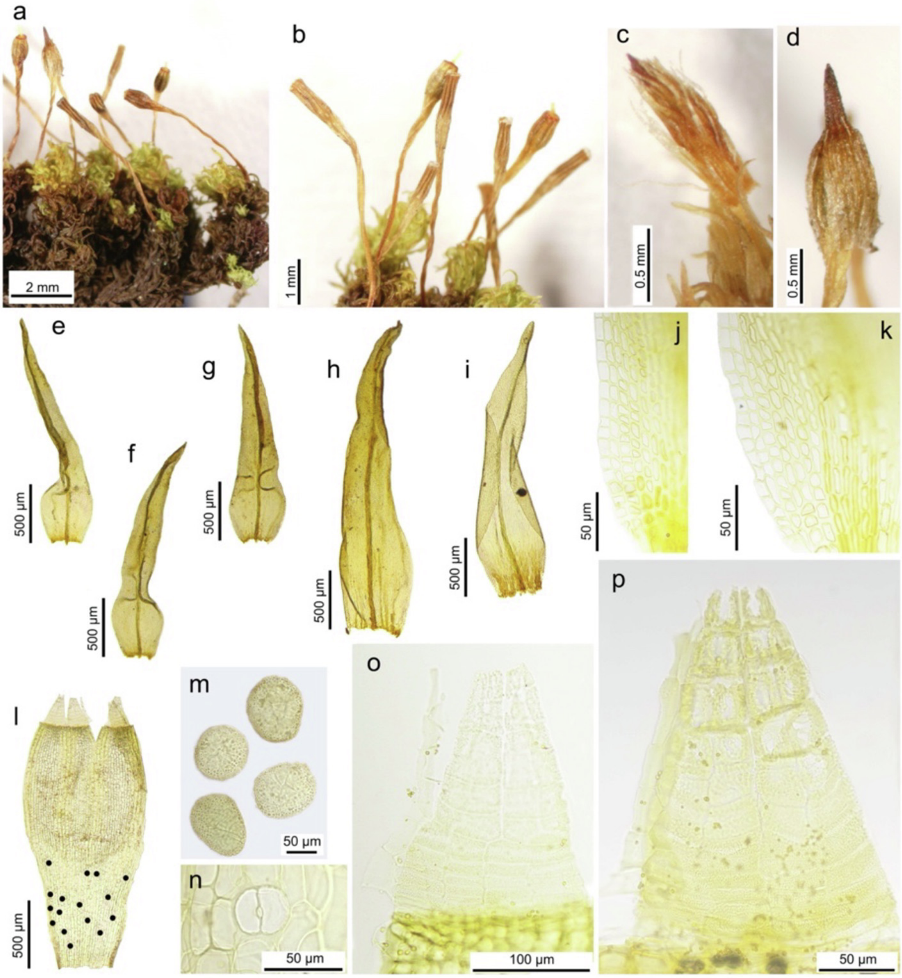


FIG. 77 – *Ulota gigantospora* F. Lara, Caparrós & Garilleti. a. Habit. b. Capsules in dry. c–d. Calyptra. e–g. Leaves. h–i. Perichaetial leaves. j–k. Marginal cells at leaf base. l. Exothecial wall, with dots indicating stoma position. m. Spores. n. Stoma. o–p. Peristome. (All from the holotype except c from the paratype in E and p from *Y. Jia 04318* [non-type, PE]).

leaf margins, short-cylindrical capsules, and narrow eight endostome segments. However, *Ulota yunnanensis* can be separated by the exostome teeth with prominent striate and almost never cancellate at the upper part, naked to sparsely hairy calyptra and smaller spores (46–71 μm). The *Ulota* species with multicellular spores also have been discussed in a previous study (Garilleti *et al.*, 2012).

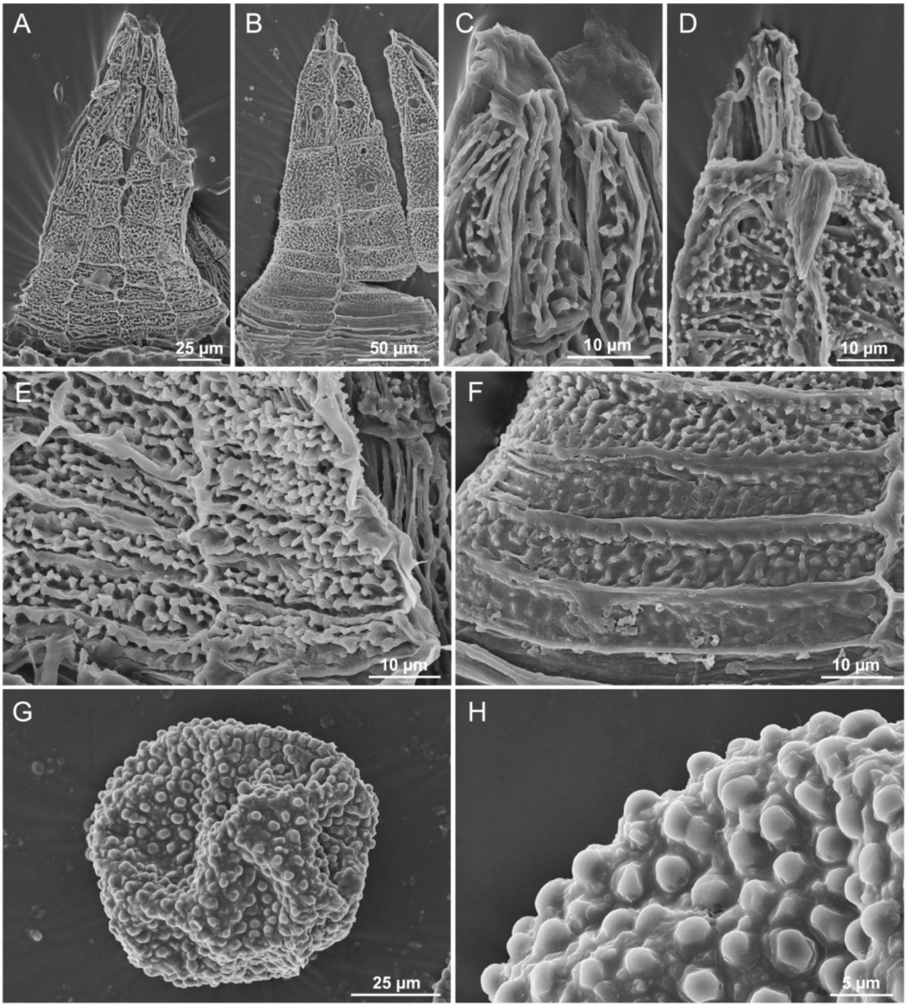


FIG. 78 – *Ulota gigantospora* F. Lara, Caparrós & Garilleti. A, outer surface of exostome; B, inner surface of exostome; C, outer surface of upper exostome; D, inner surface of upper exostome; E, outer surface of basal exostome; F, inner surface of basal exostome; G, a spore; H, surface ornamentation of a spore. (All from the holotype in E).

Key to *Ulota gigantospora* and its closely related species.

1. Endostome segments absent or sometimes rudimentary....................................2
1. Endostome segments always well-developed...3
2. Leaves small, 1.4–1.9 mm, with rounded bases; leaf basal marginal cells somewhat differentiated (3–6 rows); capsules subglobse, hardly constricted when dry; stomata located at the junction between urn and neck...........*U. yakushimensis*

2. Leaves relatively large, 1.9–2.2 mm, with ovate bases; leaf basal marginal cells hardly differentiated (often only one row); capsules cylindrical, moderately constricted when dry; stomata located on the urn........................*U. streptodon*
3. Endostome segments 16..4
3. Endostome segments 8..6
4. Endostome segments narrow, linear, smooth; leaves strongly crisped when dry..*U. novo-guinensis*
4. Endostome segments broad, lanceolate to wide-lanceolate, often slightly scabrous; leaves erect or flexuose, rarely crisped when dry......................................5
5. Leaf basal marginal cells hardly differentiated (often only one row); capsules cylindrical, with short neck that abruptly narrowed to the seta, strongly constricted when dry; endostome segments connected by some cells at lower part...*U. billbuckii*
5. Leaf basal marginal cells somewhat differentiated (3–6 rows); capsules obovate or ovate-cylindrical, with slightly long neck that gradually narrowed to the seta, variably constricted when dry; endostome segments free at the base..*U. membranata*
6. Exostome teeth with prominent striate and almost never cancellate at the upper part; calyptra naked to sparsely hairy; spores small, 46–71 μm..*U. yunnanensis*
6. Exostome teeth with densely papillose and often cancellate at the upper part; calyptra moderately hairy; spores relatively large, 87–105 μm..*U. gigantospora*

Additional Specimens Examined: **China**. SICHUAN: Jiulong Co., Lietahu, 27 Jul. 2021, *Y. Jia & L. Luo 28076* (PE), *28081* (PE), Riluku, *28108* (PE); Muli Co., 1955, *Nonglinbu 30* (PE), *36* (PE); Xiangcheng Co., 12 Aug. 1981, *X.-J. Li 9075* (KUN),

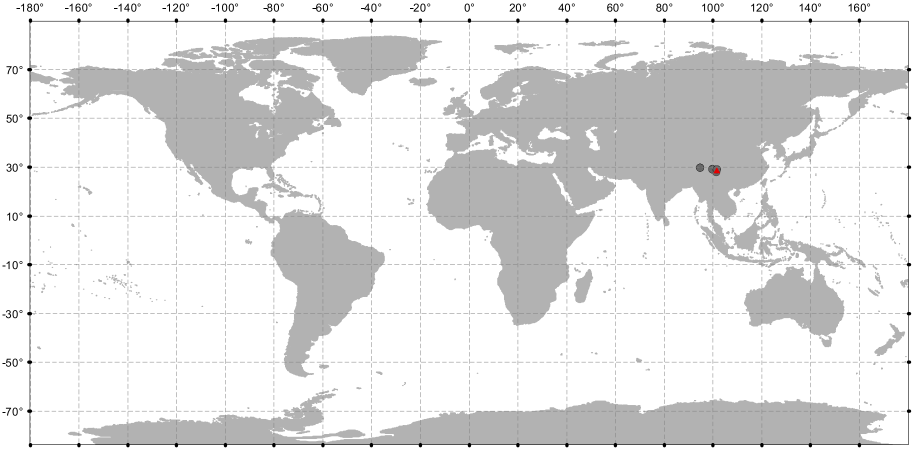


FIG. 79 – Distribution of *Ulota gigantospora* worldwide. The red triangle indicates the type locality.

16 Jul. 1998, *Y. Jia 04318* (PE), 18 Jul. 1998, *Y. Jia 04402* (PE), 29°04.977′ N, 99° 39.990′ E, 15 Jul. 2004, *Y. Jia 07293* (PE). Xizang: Linzhi, Bayi, 7 Aug. 2017, *s. coll.* (PE).

18. **Ulota gymnostoma** S.-L. Guo, Enroth & Virtanen, Ann. Bot. Fenn. 41: 459. 2004. Type: China. Hunan, Changsha Area, Liu Yang Co., Daweishan National Forest Park, along road from Lu-Yuan hotel towards Tian-Xing Hu, 25°25′ N, 114°07′30″ E, ca. 1400 m., on trunk of *Prunus persica*, 20 Sep. 2000, *Virtanan 62091* (holotype, H!).

Plants 0.5–2 cm tall, green above, brown to black below. Stems usually branched. Leaves strongly crisped when dry, erect-spreading to patent when moist, (1.6–) 2.4–3.6 (–3.9) mm long, leaf lamina lanceolate, unistratose; leaf base little wide, ovate; apex long acuminate; leaf margin plane; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (7–) 10–15 (–21) × (5–) 7–10 (–14) μm, thick-walled, nearly smooth; basal inner cells rectangular to elongate-rectangular, (18–) 29–49 (–73) × (4–) 6–7 (–9) μm, with moderately thickened wall, smooth; basal marginal cells weakly differentiated, no more than 5 rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves are somewhat longer, (3.4–) 3.7–4.2 (–4.4) mm. Vaginula is naked or sparsely hairy. Seta 2–5 mm long, twisted when dry. Capsule fully emergent to short exserted, 2.2–2.9 (–3) mm long. Urn fusiform, oblong-cylindrical or elliptical, puckered, distinctly constricted at the mouth when dry and empty, eight furrows only near the mouth and smooth below. Neck short or long, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands near the mouth, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the base of the urn or the junction of the urn and neck, or the central part of capsules. Peristome absent, sometimes rudimentary. Opercula with a short beak. Calyptra mitrate, is densely covered with long hairs. Spores spherical, finely papillose, (25–) 29–32 (–35) μm in diameter.

Illustration: Guo *et al.* (2004) and Wang and Jia (2012a); figures 80 and 81.

Habitat: It grows on trunks of trees or shrubs, such as *Liriodendron*, *Metasequoia*, pine, *Prunus*, and *Pterostyrax*. There are many records of altitude: 1200–1430 m. It sometimes grows with *Ulota crispa* together.

Distribution: It is **endemic** to China. Figure 82.

Notes: *Ulota gymnostoma* is a very distinct species by its elliptical capsules with puckered mouth and absent peristome. It is unique in Chinese *Ulota* species but very similar to *U. rhytiore* (B.H. Allen) F. Lara, Garilleti, Albertos & Mazimpaka from tropical America. Both have elliptical capsules with puckered mouth and absent peristome that are rare in the genus. However, *Ulota rhytiore* differs in the emergent capsules; the stomata are scattered throughout the urn, and the leaves strongly flexuose to spiral when dry.

No noteworthy variation was observed in *Ulota gymnostoma*.

Key to *Ulota gymnostoma* and its closely related species.

1. Capsules emergent; stomata scattered throughout the urn; leaves strongly flexuose to spiral when dry..*U. rhytiore*
1. Capsules fully emergent to short exserted; stomata restricted to the base of urn or the junction of urn and neck; leaves strongly crisped when dry...*U. gymnostoma*

Additional Specimens Examined: **China**. Anhui: Yellow Mt., 23 Aug. 1962, *X.-L. Chen 615-1* (IFP), 27 Apr. 1957, *P.-C. Chen et al. 7047a* (PE), 18 Aug. 1961, *J.-X. Luo & Z.-L. Wan 9226-2* (PE). Chongqing: Jinfo Mt., *P.-C. Chen 1793b* (PE), Aug. 1945, *C.-C. Jao K.F.33a* (PE). Fujian: Wuyi Mt., 20 Apr. 1955, *Bryophyte training class 933-e* (PE). Guangxi: Xingan Co., Maoershan Nature Reserve, 110°29′08.46″ E, 25°53′18.21″ N, 31 Mar. 2019, *Y.-M. Wei, Q.-M. Tang & Y.-B. Liao s.n.* (IBK),

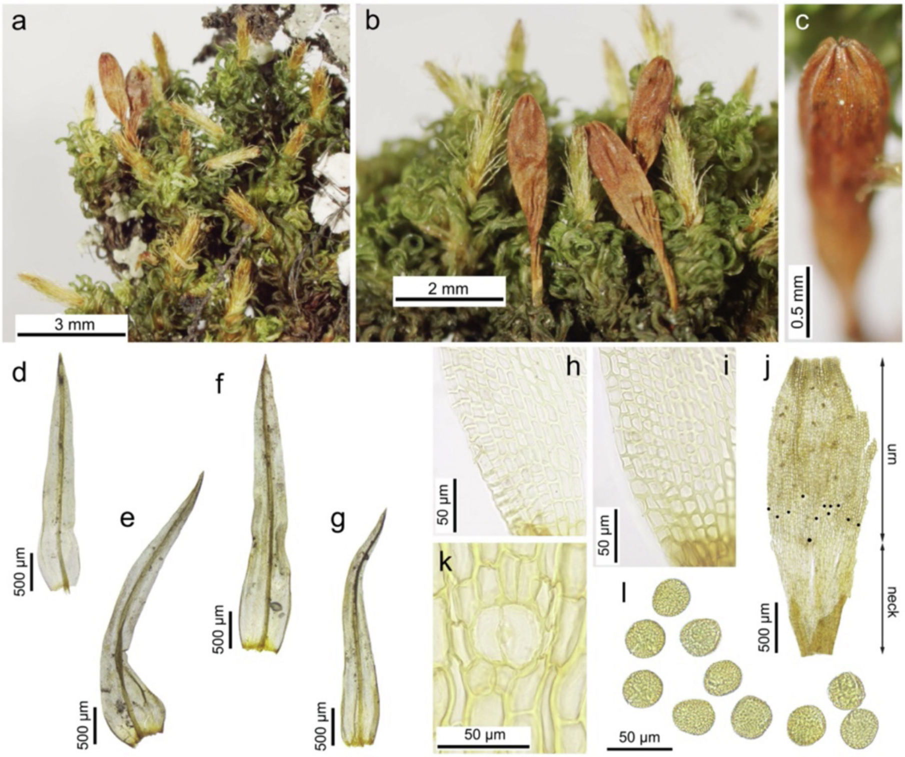


Fig. 80 – *Ulota gymnostoma* S.-L. Guo, Enroth & Virtanen. a–b. Habit. c. Puckered capsule mouth. d–e. Leaves. f. Outer perichaetial leaf. g. Inner perichaetial leaf. h–i. Marginal cells at leaf base. j. Exothecial wall, with dots indicating stoma position. k. Stoma. l. Spores. (All from the holotype except l from *P.-C. Chen 7047a* [non-type, PE]).

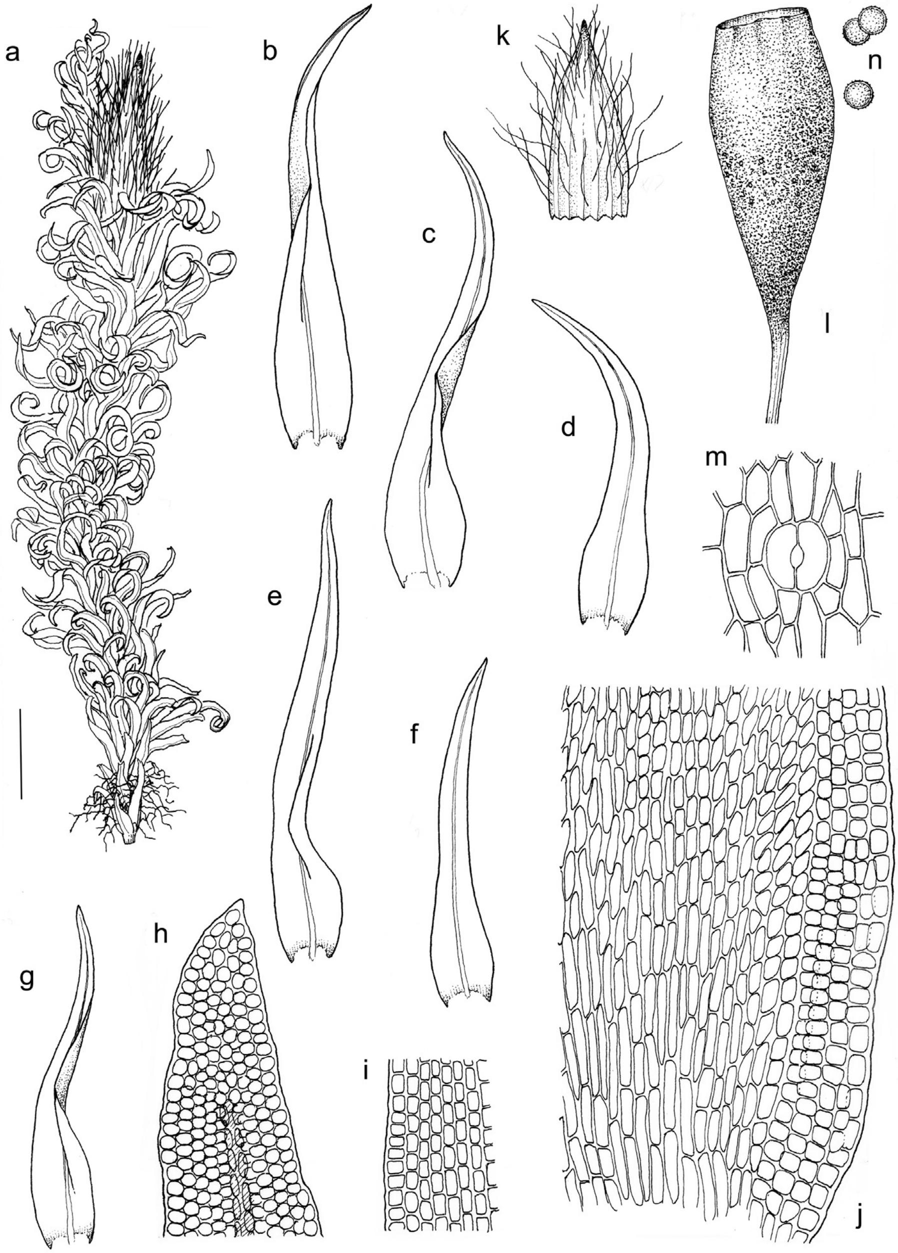


FIG. 81 – *Ulota gymnostoma* S.-L. Guo, Enroth & Virtanen. a. plant; b–f. leaves; g. perichaetial leaf; h. top laminal cells; i. median marginal cells; j. basal marginal cells; k. calyptra; l. an empty capsule in dry; m. stoma; n. spores. (Scale bar: a, k and l, 1.18 mm; b–g, 0.77 mm; h–j and m, 0.05 mm; n, 0.04 mm. All drawn from *Koponen, Huttunen, Piippo & Rao 48788* [non-type, PE]).

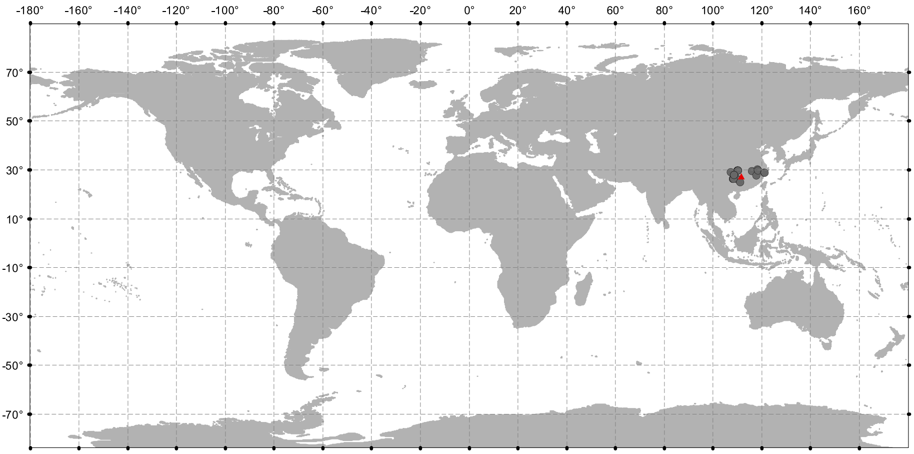


Fig. 82 – Distribution of *Ulota gymnostoma* worldwide. The red triangle indicates the type locality.

Y.-M. Wei et al. 20190331-67 (IBK); Ziyuan Co., Chetian, Shiwangutian, *Q.-M. Tang 20210619-20* (IBK). Guizhou: Jiangkou Co., Fanjingshan, 29 Jul. 1983, *Q. Gao & J.-Y. Feng 32607-1* (IFP), 24 May 2004, *X.-Y. Wang F-3098-a* (PE), 1 Apr. 2008, *Y.-X. Xiong F1346* (PE); Leishan Co., Leigongshan Nature Reserve, 27 Apr. 2006, *B.-J. Ji L060419* (PE), 14 Oct. 2005, *F. Pan L050126* (PE), 23 Apr. 2019, *T. Xu & C. Wang 20190423-1* (PE). Hunan: Sangzhi Co., Badagongshan, 26 Nov. 1999, *P.-C. Rao 58746b* (H), 20 Nov. 2000, *64910* (H), *64915* (H), *65045* (H), 24 Nov. 2000, *J. Enroth 64718* (H), *65085* (H), *V. Virtanen 61658* (H), 7 Oct. 1998, *T. Koponen, S. Huttunen, S. Piippo & P.-C. Rao 54782b* (H), *54771a* (H). Jiangxi: Lushan Botanical Garden, 25 Jun. 1955, *Bryophyte training class 142* (PE), 26 Jun. 1955, *157* (PE), Jul. 1956, *Biology department of Nanjing University 13* (PE), 16 Jun. 1956, *50* (PE). Sichuan: Jinfoshan, 8 Apr. 1935, *P.-C. Chen 1793b-1* (PE), Aug. 1945, *C. C. Jao K. F. 33a* (PE). Zhejiang: Linhai, Kuocangshan, 22 Jul. 1960, *P.-C. Wu 692-a* (IFP, PE), 2 Aug. 1960, *Q. Gao 692-1* (PE).

19. **Ulota hutchinsiae** (Sm.) Hammar, Monogr. Orthotrich. Ulot. Suec. 27. 1852. ≡ *Orthotrichum hutchinsiae* Sm., Engl. Bot. 36: 2523. 1813. ≡ *Ulotrichum hutchinsiae* (Sm.) Schimp., Bryologia Europaea 3: 1 (fasc. 46–47 Consp. vol. 3: I). 1851. *invalid, genus invalid.* Type: U.K. England, near Bantry, *Hutchins* (not located).

Orthotrichum americanum P. Beauv., Prodrome des Cinquième et Sixième Familles de l'Aethéogamie 80. 1805. ≡ *Orthotrichum anomalum* var. *americanum* (P. Beauv.) Brid., Muscologia Recentiorum Supplementum 2: 10. 1812. ≡ *Orthotrichum saxatile* var. *americanum* (P. Beauv.) Brid., Muscologia Recentiorum Supplementum 2: 10. 1812. ≡ *Weissia americana*

(P. Beauv.) Lindb., Journal of Botany, British and Foreign 11: 200. 1873. ≡ *Ulota americana* (P. Beauv.) Limpr., Die Laubmoose Deutschlands, Oesterreichs und der Schweiz 2: 21. 1891. *illegitimate, later homonym.* TYPE: America, *Mühlenberg 87* (lectotype, G).

Orthotrichum crispum var. *brevifolium* Wahlenb., Flora Suecica 2: 735. 1826.

Orthotrichum hudchinsianum Schleich., Cat. Pl. Helv. ed. 4: 42. 1821. *nom. inval. err. pro. O. hutchinsiae.*

Orthotrichum hutchinsiae var. *nigrescens* Hook. & Grev., Edinb. Jour. Sci. 1: 125. 1824. *nom. illeg.*

Orthotrichum nigricans Brid. ex Limpr. in Rabenh., Deutschl. Crypt. Fl. 4 (2): 21. 1890. *nom. invalid.*

Orthotrichum strictum Brid., Bryologia Universa 1: 289. 1826. TYPE: U.S.A. Massachusetts, *Cooley 25*, 1820 (holotype, B!).

Ulota nigricans Brid., Bryologia Universa 1: 792. 1827. TYPE: CANADA. Terre Nueve, *LaPylaie*, 1825 (holotype, B!).

Plants 0.5–1.5 cm tall, yellowish green to green apex, brown to black below. Stems usually branched. Leaves erect-appressed, slightly flexuose near apex when dry, erect-spreading to patent when moist, (1.3–) 1.5–1.8 (–2.2) mm long, leaf lamina lanceolate, unistratose; leaf base more or less wide, ovate; apex acuminate; leaf margin plane or weakly recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (5–) 7–9 (–13) × (4–) 6–8 (–10) μm, thick-walled, often with 1–3 low simple papillae per cell; basal inner cells linear, rectangular to elongate- rectangular, (10–) 19–32 (–49) × (1–) 2–3 (–4) μm, with strongly thickened wall, smooth; basal marginal cells not differentiated or weakly differentiated into no more than 3 rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves much longer, 2.4–2.9 mm. Vaginula is naked or sparsely hairy. Seta (2–) 2.6–3.5 (–4.5) mm long, twisted anticlockwise when dry. Capsule long exserted, ca. 1.7 mm long. Urn cylindrical, slightly to moderately constricted below the mouth when dry and empty, with eight furrows along the entire length. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the base of the urn or the junction between the urn and neck. Preperistome rarely seen. Peristome double. Exostome teeth 16, often united into 8 pairs, reflexed when dry, often lying on the exothecium, rarely erect or spreading, lanceolate, densely papillose to papillae-striate near apex on the outside, papillose to papillae-striate to striate on the inside. Endostome segments 8, linear to narrow-lanceolate, 2/3 to almost reaching the exostome teeth, partially biseriate, hyaline, smooth outside, scabrous inside. Opercula with a short to medium-long beak. Calyptra mitrate, moderately to strongly densely hairy. Spores spherical, finely papillose, (11–) 13–14 (–16) μm in diameter.

Illustration: Nyholm (1960), Smith (1978), Crum and Anderson (1981), Ireland (1982) and Ignatov and Ochyra (1994); figures 83 and 84.

Habitat: It grows on rocks, rarely on trees, such as birch and *Fagus* (beech). There are many records of altitude: (0–) 522–1090 (–1900) m. It is sometimes mixed with *U. crispa*, *U. curvifolia*, and *Orthotrichum sp.*

Distribution: It is common on both sides of the northern Atlantic and tends to spread inland, including Austria, Canada, Finland, France, Germany, Ireland, Norway, Poland, Sweden, Switzerland, U.K. and U.S.A. There is only one locality in Asia from the Altai region based on a previous study (Ignatov and Ochyra, 1994). The new record in Japan is probably misidentification and see below for detail. Figure 85.

Notes: *Ulota hutchinsiae* is easily distinguished by the erect-appressed leaves, hardly differentiated basal marginal leaf cells, and eight narrow endostome segments. The first two features make *Ulota hutchinsiae* look like *Orthotrichum*; combining the exserted cylindrical capsules, small spores, and saxicolous habit, it is most like *O. anomalum* Hedw. But *Orthotrichum anomalum* differs in having prominently striate exostome teeth, absent endostome segments, and immersed stomata.

In habit, *Ulota hutchinsiae* resembles *U. curvifolia*, they are both saxicolous mosses and morphologically share non-crisped leaves and weakly differentiated leaf basal marginal cells. However, *Ulota curvifolia* differs in erect to flexuose leaves, high leaf laminal papillae, short-cylindrical capsules (*vs.* cylindrical), strongly striate exostome teeth, and relatively large spores (19–24 μm).

Ulota hutchinsiae in Asia has been reported from the Altai region (Ignatov and Ochyra, 1994) and recently from Japan (Suzuki and Iwatsuki, 2011). Based on their descriptions, the Altai population (*Bardunov*, MHA, IRK) is consistent with our observation of *Ulota hutchinsiae*, but the Japanese materials (*T. Suzuki 60666 & 60668*, NICH) are probably identified incorrectly, although we have not seen them yet. Their small plants in size (3–4.8 mm), large spores (19–22 μm), short seta (1–2.3 mm), and tree-growing habit do not agree with *Ulota hutchinsiae* obviously, but more like *Orthotrichum* species, so does the leaf shape shown in the illustration provided by the authors.

No noteworthy variation was observed in *Ulota hutchinsiae.*

Key to *Ulota hutchinsiae* and its closely related species.

1. Stomata immersed; endostome segments absent.......................... *O. anomalum*
1. Stomata superficial; endostome segments well-developed................................2
2. Leaves erect to stiffly flexuose when dry; middle and upper leaf cells with prominent conic or forked papillae; exostome teeth strongly striate; spores relatively large, 19–24 μm; capsules short-cylindrical when dry.. *U. curvifolia*
2. Leaves erect-appressed when dry; middle and upper leaf cells with short papillae; exostome teeth densely papillose; spores smaller, 13–14 μm; capsules cylindrical when dry.. *U. hutchinsiae*

Additional Specimens Examined: **Austria**. Tryol: Ötztal, 30 Jun. 1901, *E. Bauer s.n.* (H); Trins, valle Gschnitz, *A. Kerner s.n.* (H).

Canada. NEW BRUNSWICK: Grand Manan Island, 9 Jun. 1822, *W. R. Taylor 6077* (MICH), *6093* (MICH). NEWFOUNDLAND: Avalon Peninsula, 27 May 1975, *G. R. Brassard 10091* (H), 3 Jul. 1975, *A. J. Fife 1008* (MICH); Bonavista North, 27 Aug. 1949, *R. Tuomikoski 6029* (H); Fortune Bay, 23 Jun. 1972, *J. A. Hancock 423* (MICH); Grand Falls, 2 Sep. 1949, *R. Tuomikoski 6069* (H, MICH), *6081* (H, MICH), 16 Jul. 1956, *T. Ahti s.n.* (H); Placentia Bay, Pipers Hole River, 24 Jun. 1975, *G. R. Brassard, A. J. Fife and D. Weber 985* (H), *G. R. Brassard 10234* (MICH); Rencontre West, 20 Jun. 1949, *R. Tuomikoski 1315* (H); Steady Brook, 10 Jul. 1949, *R. Tuomikoski 2850* (H). NOVA SCOTIA: Anapolis Co., Kejimkujik National Park, 2 Aug. 1968, *R. R. Ireland 12442* (MICH), 3 Aug. 1968, *12528* (MICH), 4 Aug. 1968, *12614* (H); Halifax Co., Laurie Provincial Park, 25 Jul. 1968, *R. R. Ireland 12201* (MICH); Lunenburg Co., 20 Jul. 1974, *R. R. Ireland 17585* (MICH), 22 Jul. 1974, *17694* (H). ONTARIO: Algoma Distr., 6 Aug. 1958, *R. F. Cain s.n.* (MICH), 3–4 Aug. 1971, *R. R. Ireland 14830* (H, MICH); Cochrane Distr., 6 Jun. 1984, *R. R. Ireland 21576* (H, MICH); Davis Lock between Lake Opinicon and Sand Lake, 13 Jul. 1990, *R. R. Ireland 24501* (H); Kenora Distr., 11 Jul. 1982, *D. H. Vitt s.n.* (H, HBG); Leeds and Grenville United Co., 13 Jul. 1990, *R. R. Ireland 24501* (H, MICH); Renfrew Co., 20 Apr. 1987, *L. M. Ley 647* (MICH); Rosseau, 26 Jul. 1987, *R. R. Ireland 23053* (H, MICH); Thunder Bay Dist., 19 Aug. 1971, *R. R. Ireland 15528* (H, MICH, UBC), 30 Oct. 1979, *C. E. Garton 19299* (MICH), 19 Aug. 1971, *R. R. Ireland 15528* (H, UBC), 5 Jun. 1969, *C. E. Garton 11642* (H), 30 Oct. 1979, *C. E. Garton 19299* (H, MICH). QUEBEC: Charlevoix Co., 1945, *M. Raymond & J. Kucyniak s.n.* (MICH); Pontiac Co., 16 Jun. 1972, *R. R. Ireland 16186* (MICH); Richmond Gulf, 3 Jul. 1939, *J. Marr M321* (MICH).

Finland. ÅLAND: s. loc., *J. O. Bomansfon* (NSW). KYMENLAAKSO: N. Elimä, Pelkuanmäki, Nov. 1903, *H. Buch s.n.* (H); Sippola, Enäjärvi, 9 Jul. 1969, *Lars Fagerström s.n.* (H); Sunila, 9 Feb. 1918, *V. K. s.n.* (H). PIRKANMAA: Ruovesi, Kauttu, 26 Jul. 1946, *Niilo Söyrinki s.n.* (H). UUSIMAA: Bromarv, Framnäs, 27 Jun. 1904, *H. Buch s.n.* (H), 29 Jun. 1904, *s.n.* (H); Kaivopuisto, 30 Oct. 1866, *J. A. Palmén s.n.* (H).

France. NOUVELLE-AQUITAINE: Basque, Mt. Mondarrain, *V. P. Allorge s.n.* (PC). BRETAGNE: Brest, *L. Bason* (NSW). GRAND EST: Vosges Mt., Jul. 1898, *T. Herzog* (NSW), Aug. 1867, *Piérrat* (NSW).

Germany. BAVARIA: Mt. Rudolfstein, *Funck 22* (JE), *531* (JE). SAARLAND: Mettlach, Oct. 1866, *F. Winter s.n.* (HBG).

Ireland. CONNACHT: 12 May 1876, *S. A. Steuad s.n.* (H). MUNSTER: Brandon Mt., Aug. 1935, *Kerry s.n.* (MICH); Cork Co., 27 Aug. 1979, *A. C. Crundwell s.n.* (MICH).

Norway. HORDALAND: Etne, 17 Jun. 1971, *E. & P. Hegewald 3607* (MO); Granvin, 30 Jun. 1957, *T. Ahti B744* (H). MØRE OG ROMSDAL: Christiansund, Oct. 1868, *P. G. Lorentz s.n.* (HBG). ROGALAND: Egersúnd, Jul. 1889, *N. Bryhn s.n.* (NSW).

Sweden. ÖSTERGÖTLAND: Krokek, 20 Apr. 1894, *A. Grape s.n.* (H). SMÅLAND: Burseryd, Jun. 1877, *K. A. T. Seth s.n.* (H3150843, H3150866, H3150867). SÖDERMANLAND: Huddinge, 18 Jun. 1898, *A. Arvén s.n.* (MICH). UPPLAND: Gottsunda, 22 May 1855, *J. E. Zetterstedt s.n.* (H). VÄSTMANLAND: Viker, 18 Aug. 1966, *T. Koponen 10666* (H).

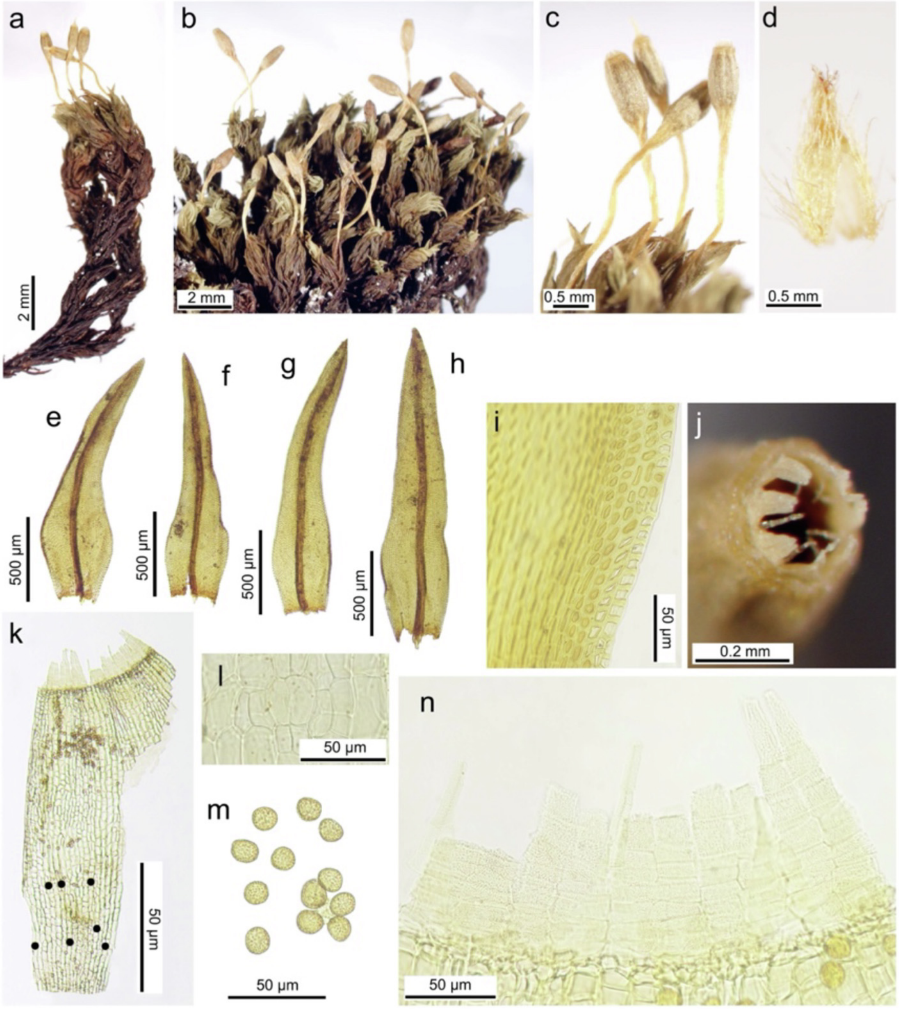


FIG. 83 – *Ulota hutchinsiae* (Sm.) Hammar. a–b. Habit. c. Capsules in dry. d. Calyptra. e–h. Leaves. i. Marginal cells at leaf base. j. Capsule mouth viewed from above. k. Exothecial wall, with dots indicating stoma position. l. Stoma. m. Spores. n. Peristome with most teeth broken. (a–d, j from *D. H. Vitt* [non-type, PE], e–i and k–m from *R. R. Ireland 15528* [non-type, UBC]).

Switzerland. BERNER OBERLAND: Guttannen, Sep. 1904, *P. F. Culamann s.n.* (MICH). TICINO: Faido, Jul. 1895, *Röll* (NSW).

U.K. ENGLAND: Dartmoor, Devon, 8 Apr. 1884, *W. B. Waterfall* (NSW), *320-1* (NSW). SCOTLAND: Killin, *E. Hunt s.n.* (H); Lochan na Lairige, 4 Aug. 2000, *F. R. Lammiman & C. Rieser s.n.* (BBSUK); Mid Ebudes, 1998, *P. J. Chamberlain s.n.* (E00350361, E00350357); New Galloway, Sep. 1850, *J. Mc. Andrew s.n.* (NSW),

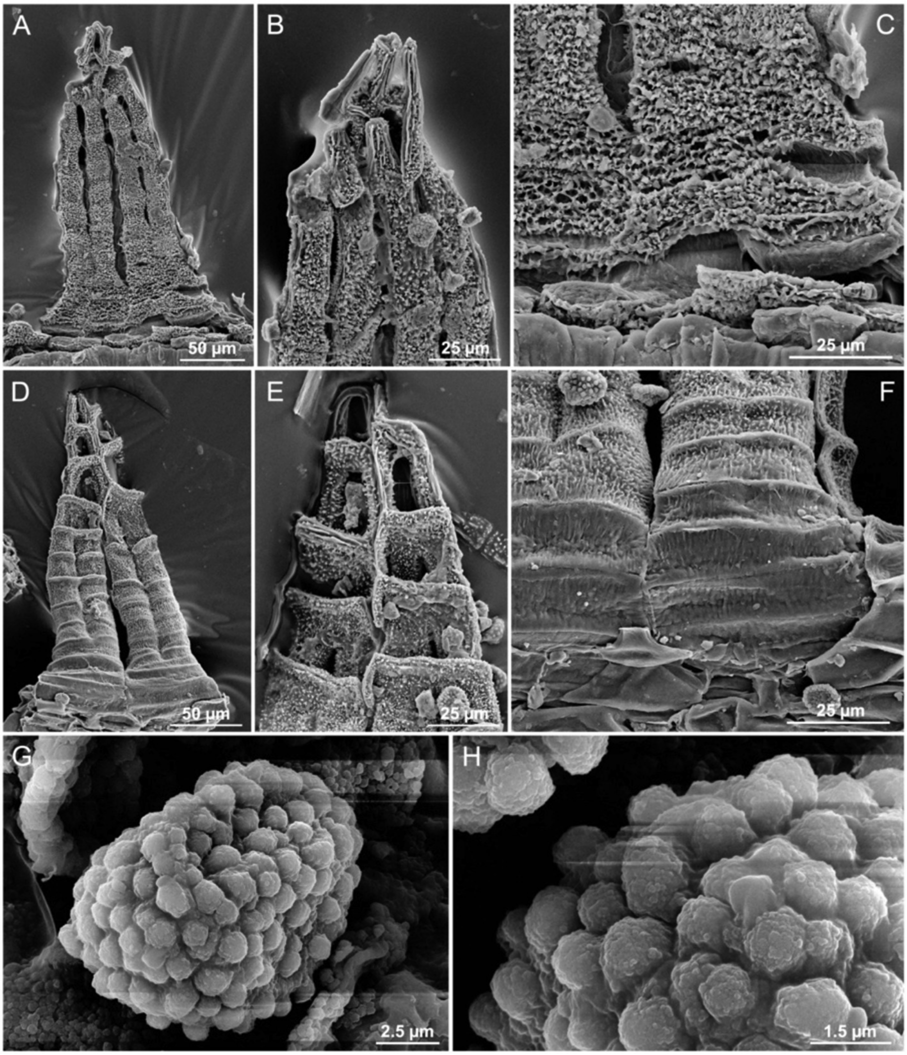


FIG. 84 – *Ulota hutchinsiae* (Sm.) Hammar. A, outer surface of exostome; B, outer surface of upper exostome; C, outer surface of basal exostome; D, inner surface of endostome; E, inner surface of upper exostome; F, inner surface of basal exostome; G, a spore; H, surface ornamentation of a spore. (All from a non-type specimen in M [M-0155420]).

Aug. 1890, *s.n.* (HBG); North Ebudes, 19 Jun. 1967, *H. J. Birks s.n.* (E), 14 Aug. 1968, *H. J. Birks s.n.* (E), 18 Aug. 1968, *C. C. Townsend s.n.* (E); Perthshire, 7 Sep. 1836, *C. Challeach s.n.* (MICH).

U.S.A. ALABAMA: Dekalb Co., 6 Sep. 1968, *D. H. Vitt 1247* (MICH). ALASKA: Yakutat, 14 Jul. 1945, *L. D. Stair 4882* (MICH). ARIZONA: Sauta Batalua Mt., 24 Oct. 1924, *E. B. Bartram 106* (H). ARKANSAS: Bald Knob, 12 Feb. 1922,

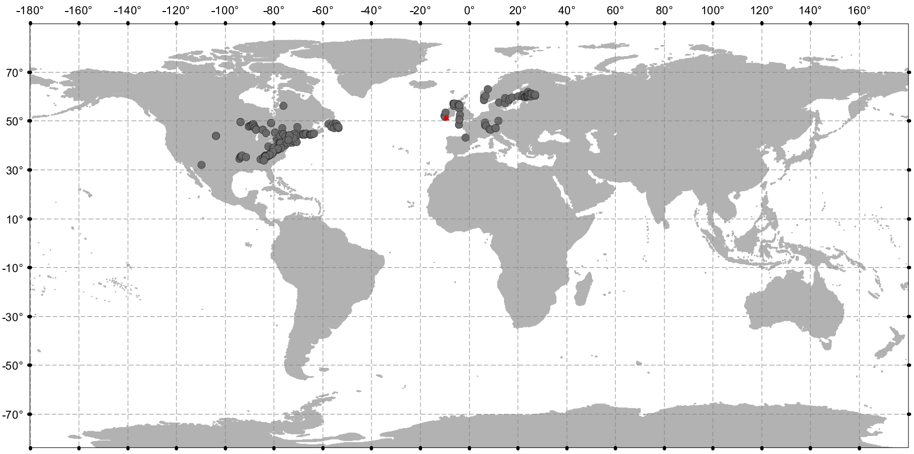


FIG. 85 – Distribution of *Ulota hutchinsiae* worldwide. The red triangle indicates the type locality.

W. R. Taylor 6911 (MICH); Franklin Co., 4 Jun. 1953, *L. E. Anderson 12102* (MICH); Magazine Mt., 30 Jun. 1934, *W. H. Welch 2903* (MICH); Newton Co., 4 Oct. 1985, *B. H. Allen & R. E. Magill 4757* (H), 24 Apr. 1993, *P. L. Redfearn, Jr. & A. Redfearn s.n.* (H, MICH), 2 Feb. 1963, *P. L. Redfearn, Jr. 11851* (MICH); Polk Co., 20 Mar. 1965, *P. L. Refearn, Jr. 17226* (MICH). CONNECTICUT: Windham Co., 3 Oct. 1943, *H. A. Gleason, Jr. s.n.* (MICH); Valley Forge, 17 Apr. 1939, *W. S. Allen & L. D. Stair s.n.* (MICH). GEORGIA: Stone Mt., Aug. 1893, *J. K. Small s.n.* (H, MICH). MAINE: Hancock Co., 22 Jul. 2006, *W. B. Schofield 124628* (UBC); Mt. Desert, 9 Sep. 1920, *W. R. Taylor 3316* (MICH); Oxford, 1 Aug. 2006, *P. Ledlie 5101* (MO); Waldo Co., 3 Jul. 1942, *E. C. Ogden 2458* (MICH); Washington Co., 1 Jul. 2008, *B. Shaw 7997* (DUKE), *D. D. Davis 580* (MO). MASSACHUSETTS: S. B. Reservoir, 23 Dec. 1894, *G. G. Kennedy 734* (MICH). MICHIGAN: Chippewa Co., Sugar Island, Jun. 1933, *W. C. Steere 3200* (MICH), *3324-2* (MICH); Keweenaw Co., 26 Jun. 1981, *F. J. Hermann 29023* (H, MICH), 14 May 1949, *C. D. Richards 37* (MICH); Margauette Co., 15 Jun. 1933, *A. H. Smith s.n.* (MICH), 20 Aug. 1936, *W. C. Steere s.n.* (MICH), 29 Aug. 1936, *W. C. Steere s.n.* (MICH); Scoville Point, 2 Jul. 1930, *A. H. Povah 48* (MICH). MINNESOTA: Cook Co., 1902, *J. M. Holzinger s.n.* (MICH), 16 Aug. 1960, *W. A. Olson 707* (MICH); Grand Marais, 5 Jul. 1904, *J. M. Holzinger s.n.* (MICH). NEW HAMPSHIRE: Carroll Co., 19–24 Apr. 1908, *H. H. Barlett 1249* (MICH); Cheshire Co., 11 Aug. 1918, *W. R. Taylor 2874* (MICH); Lake Winnipesaukee, Apr-Jul. 2004, *A. F. Bradley 1421* (MO); Marlow, 3 Aug. 1939, *W. S. Allen & L. D. Stair s.n.* (MICH). NEW JERSEY: Morris Co., Green Pond Mt., 31 Mar. 1918, *W. R. Taylor 2646* (MICH). NEW YORK: Buffalo, *s.coll.* (MICH535901, MICH535932); Delaware Co., 21 Feb. 1953, *K. L. Brooks 2104* (MICH), 9 May 1959, *S. J. Smith 28134* (MICH); Essex Co., 15 Aug. 1956, *S. J. Smith 21215* (MICH), 21 Aug. 1957, *F. J. Hermann 13937* (MICH). Greene Co., 18 Jun. 1952, *S. J. Smith 11506* (MICH), 8 Aug. 1968, *43096* (H); Morris Co., 31 Mar. 1918, *W. R. Taylor 2646* (MICH); Suffolk Co., 10 May 1914, *R. Latham s.n.*

(MICH); Washington Co., 21 May 1954, *S. J. Smith 16096* (MICH). North Carolina: Avery Co., 1 Apr. 1978, *J. Rohrer 479* (MICH), *453* (MICH), *533* (MICH); Buncombe Co., 29 Apr. 1978, *D. H. Vitt & D. G. Horton s.n.* (H), 29 Jun. 1978, *D. H. Vitt & D. G. Horton s.n.* (HBG, MICH); Burke Co., 27 May 1964, *L. E. Anderson 15067* (MICH); Grandfather Mt., 13 Jun. 1936, *A. J. Sharp 337* (MICH); Macon Co., 2 Aug. 1952, *L. E. Anderson 11242* (H); Mitchell Co., 24 Aug. 1950, *L. E. Anderson & E. F. Jones 9392-2* (MICH); Transylvania Co., 21 Sep. 1968, *D. H. Vitt 1400* (MICH); Watauga Co., 6 Jun. 1978, *J. Rohrer 496* (MICH); Yancey Co., 8 Jun. 1964, *L. E. Anderson 15218* (MICH), May 1977, *H. Crum s.n.* (H), 8 Jun. 1964, *L. E. Anderson 15239* (MICH). Ohio: Hocking Co., 26 Jul. 1942, *R. T. W. 3232* (MICH). Pennsylvania: Bradford, 7 Nov. 2008, *S. Munch 08049* (MO); Clinton, *B. Allen 27069* (MO), 3 Aug. 2002, *B. Allen 24826* (MO), 16 Jun. 2004, *26778* (MO), 26 Jul. 2003, *R. A. Pursell 12406* (MO). Rhode Island: Smithfield, Wolf Hill, 15 Apr. 1933, *J. E. Collins s.n.* (MICH). South Dakota: Great Plains, Black Hills, 24 May 1977, *S. P. Churchill 8946* (H, MICH). Tennessee: Blount Co., 5 Mar. 1953, *A. J. Sharp 533* (MICH); Greene Co., 4 Jun. 1978, *T. Patrick & B. C. Nichols 1176* (MICH); Mt. Polk Co., 19 Mar. 1939, *A. J. Sharp 3964* (MICH); Page Co., 15 May 1986, C. T. Bryson 3007 (MICH); Ramsey Cascades, 4 Sep. 1947, *W. C. Steere 10326* (MICH); Sevier Co., 20 Jul. 1934, *A. J. Sharp 3456* (MICH), 19 Jun. 1958, *W. B. Schofield 8732* (H, MICH), 19 Jul. 1958, *W. B. Schofield 8833* (H, MICH); Smoky Mts., 6 Sep. 1947, *W. C. Steere 10599-1* (MICH). Vermont: Monadnock Mt., 25 Aug. 1956, *H. Crum & L. Anderson 7913* (MICH); Newfane, 1 Aug. 1921, *s.coll.* (MICH); Willoughby, 23 May 1905, *s.coll.* (MICH). Virginia: Barbour Co., 20 May 1939, *F. W. Gray 7521* (MICH), *s.n.* (MICH); Bull Run Mt., 27 Aug. 1938, *E. C. Leonard 18104* (MICH); Giles Co., 20 Jul. 1936, *M. E. Pierce s.n.* (MICH536973, 536975); Grayson Co., 3 May 1969, *D. H. Vitt 1454* (MICH); Langley, 15 Mar. 1903, *E. B. Chamberlain 1292* (MICH); Malkers Mt., 20 May 1892, *A. M. Vail & E. G. Britton s.n.* (MICH); Page Co., 28 Apr. 1969, *D. H. Vitt 1433* (MICH), *1435a* (MICH), Shenandoah National Park, 13 Jun. 1944, *I. Schnooberger 4501* (MICH), *4534* (MICH), 15 Jun. 1944, *4703* (MICH), 15–16 Jun. 1944, *4883* (MICH), 16 Jun. 1944, *4830* (MICH), *F. E. Wynne 3032* (MICH), 17 Jun. 1944, *F. E. Wynne 3128* (MICH), *I. Schnooberger 4945* (MICH), 18 Jun. 1944, *4997* (MICH), 19 Jun. 1944, *F. E. Wynne 3208* (MICH), *I. Schnooberger 5071* (MICH), 22 Jun. 1944, *5229* (MICH), 23 Jun. 1944, *F. E. Wynne 3318* (MICH), *I. Schnooberger 5381* (MICH), 24–25 Jun. 1944, *5490* (MICH), 26 Jun. 1944, *5557* (MICH), 29 Jun. 1944, *F. E. Wynne 3483* (MICH); Rappahannock Co., 24 Oct. 1957, *F. J. Hermann 14163* (MICH); Warren Co., 28 Apr. 1969, *D. H. Vitt 1428* (MICH); s. loc., 15 Aug. 1942, *L. B. Henderson 522* (DUKE).

20. **Ulota intermedia** Schimp., Syn. Musc. Eur. (ed. 2) 305. 1876. ≡ *Orthotrichum ulophyllum* var. *intermedium* (Schimp.) Kindb., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 7(9): 121. 1883. ≡ *Ulota crispa* var. *intermedia* (Schimp.) Cardot, Bull. Soc. Roy. Bot. Belgique 24(2): 26. 1885. ≡ *Weissia ulophylla* var. *intermedia* (Schimp.) Braithw., Brit. moss Fl. 2: 94. 1889. *Illegitimate, earlier name included.* ≡ *Weissia intermedia*

(Schimp.) Tolf, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 16 Afd. 3(9): 70. 1891. ≡ *Orthotrichum ulophyllum* ssp. *intermedium* (Schimp.) Kindb., Eur. N. Amer. Bryin. 2: 307. 1897. ≡ *Ulota crispa* ssp. *intermedia* (Schimp.) Hérib., Mém. Acad. Sci. Clermont-Ferrand 14: 333. 1899. ≡ *Orthotrichum intermedium* (Schimp.) Kindb. ex Paris, Index bryol. (ed. 2) 3: 331. 1905. *nom. inval.* ≡ *Ulota ulophylla* var. *intermedia* (Schimp.) Jansen & Wacht., Ned. Kruidk. Arch. 53: 215. 1943. TYPE: "in Hassia superior ad Fagos male evolutas (BRUCH), prope *Jever* Oldenburgiae, ipse copiose legi ad arborum, praeprimis Fraxini et Aceris truncus in valle Scotiae *Loch Lomond*." GERMANY. Hesse, Marburg-Biedenkopf, "Ludwigshütte. Jul. Aug. 41. *Bruch* m. Nov. 41" (lectotype, BM000852210, designated by Caparrós *et al.*, 2016).

Plants 1–1.5 cm tall, green above, brown to black below. Stems usually branched. Leaves strongly crisped when dry, patent to wide-spreading when moist, (2.2–) 2.4–3.0 (–3.4) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex acuminate; leaf margin plane or partially recurved; costa strong, ending near the apex. Upper and middle laminal cells irregularly rounded, sometimes oblong, (7–) 10–15 (–17) × (6–) 8–10 (–13) μm, thick-walled, with 1–2 short papillae per cell on both surfaces; basal inner cells rectangular, elongate-rectangular to vermicular, (20–) 27–36 (–47) × (4–) 5–7 (–8) μm, with strongly thickened walls, smooth; basal marginal cells often differentiated in (2–) 5–9 (–11) rows hyaline cells, quadrate to rectangular, with thickened transverse walls.

Autoicous. Perichaetial leaves much differentiated, (3.1–) 3.2–3.8 (–3.9) mm. Vaginula is naked or hairy. Seta (2–) 2.5–4 (–4.5) mm long, twisted anticlockwise when dry. Capsule short to long exserted, 1–2 mm long. Urn cylindrical to short-cylindrical when dry and empty, hardly constricted below the mouth when dry, 8-ribbed the entire length. Neck short or long, abruptly or gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction of urn and neck. Preperistome rarely seen. Peristome double. Exostome teeth 16, united into 8 pairs, lanceolate, densely papillose throughout or striate near apex on the outside, papillose above and striate below on the inside, reflexed when dry and lying on the exothecium. Endostome segments 8, linear to linear-lanceolate, hyaline, uni- or partially bi-seriate, ca. 1/4 width of teeth in the middle part, smooth outside, slightly scabrous, rarely smooth inside, almost as long as teeth. Opercula with a short to medium-long beak. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (17–) 22–28 (–36) μm in diameter.

Illustration: figure 86.

Habitat: It grows on trees, and only one phorophyte was recorded, *i.e. Alnus*. There are a few records of altitude: 1200 m.

Distribution: It sporadically occurs in North Hemisphere, including Austria, Canada, China, France, Germany, Japan, Norway, Sweden, and U.K. Figure 87.

Notes: *Ulota intermedia* has been considered a variety or subspecies of *U. crispa* for a long time until recently. Caparrós *et al.* (2016) reinstated the species rank of

Ulota intermedia based on molecular and morphological evidence. Some authors subsequently followed this treatment (Fedosov and Ignatova, 2018; Blockeel, 2017), and so do we, although the key provided by Caparrós *et al.* (2016) is not always easy to use during our study.

Caparrós *et al.* (2016) stated that *Ulota intermedia* differs from *U. crispa* in the capsules that are not or weakly constructed when dry and empty and linear-lanceolate endostome segments with distinctly thickened and prominent cross-walls on the inside surface. Additionally, *U. intermedia* is also similar to *U. crispula*, but the latter is distinguished by the leaves slightly to moderately crisped when dry and slender linear endostome segments, often with thin cross-walls on the inside surface.

Key to *Ulota intermedia* and its closely related species.

1. Capsules moderately to strongly constricted below the mouth when dry and empty.. *U. crispa*
1. Capsules hardly or slightly constricted below the mouth when dry and empty..2
2. Leaves flexuous, slightly to moderately crisped when dry; endostome segments linear, slender and fragile, often with thin cross-walls on the inside surface.. *U. crispula*
2. Leaves strongly crisped when dry; endostome segments linear to linear-lanceolate, not fragile, often with distinctly thickened and prominent cross-walls on the inside surface.. *U. intermedia*

Additional Specimens Examined: **Austria**. Salzburg: 9 Aug. 1953, *J. Froehlich s.n.* (S). Styria: Schladming, alt. 1200 m, 7 Aug. 1876, *J. B. Seidler s.n.* (H).

Canada. British Columbia: Moresby Island, Queen Charlotte Islands, 52°45′ N, 132°07′ W, 1 Aug. 1968, *W. B. Schofield 37469* (UBC). Newfoundland: Miquelon, *Dr. Delamare s.n.* (HBG, NSW, H). Ontario: Ottawa, *s.coll.* (H).

China. Guizhou: Daozhen Co., 2 Aug. 2003, *M.-Z. Wang 59104-1* (PE). Sichuan: Jiulong Co., Gongga Mountain Nature Reserve, 14 Apr. 2021, *Q.-H. Wang 2515-1* (PE), 15 Apr. 2021, *2545c* (PE); Luding Co., Hailuogou National Glacier Forest Park, 16 Apr. 2021, *Q.-H. Wang 2557* (PE), *2568* (PE), *2585-1* (PE), 17 Apr. 2021, *2638* (PE), Yanzigouzhen, 18 Apr. 2021, *Y. Jia & L. Luo 20595* (PE); Xiaojin Co., 30 Jul. 2007, *Y. Jia 09545* (PE).

France. Grand Est: Vosqes Mts., 3 Aug. 1883, *s.coll.* (NSW). Normandie: Cherbourg, Jun. 1884, *L. Corbière s.n.* (NSW).

Germany. Baden-Württemberg: Rufenholzplatz, Seebachtal, 20 Oct. 1861, *F. Elmendorff s.n.* (HBG). Thuringia: illegible handwritten locality, 25 Jul. 1880, *Z. K. Schliephacke s.n.* (HBG).

Japan. Mie: Suzuka Mts., Shakaga-dake, alt. ca. 1090 m, 23 Nov. 1951, *N. Takaki s.n.* (S). Nagano: Mt. Kisokoma, 9 Jul. 1947, *N. Takaki 3745* (S).

Norway. Oppland: Sjårdalen, alt. 100 m, Jul. 1892, *N. Bryhn s.n.* (NSW). Rogaland: Stavanger, alt. 10 m, Jul. 1902, *N. Bryhn s.n.* (NSW); alt. 5 m, Jul.

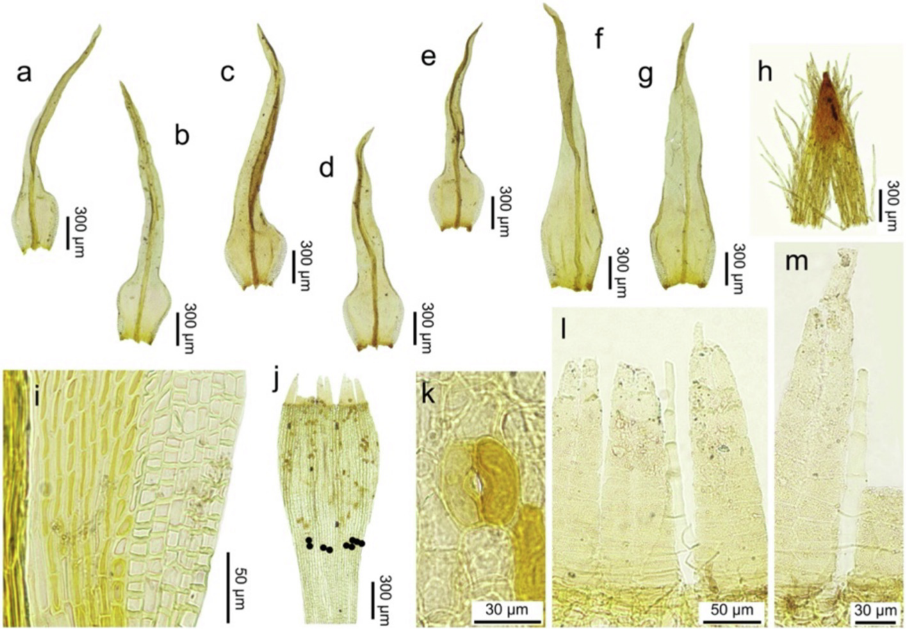


FIG. 86 – *Ulota intermedia* Schimp. a–e. Leaves. f–g. Perichaetial leaves. h. Calyptra. i. Marginal cells at leaf base. j. Exothecial wall, with dots indicating stoma position. k. Stoma. l–m. Peristome. (All from Norway, *N. Bryhn s.n.* [non-type, NSW] except c–e from France, *Dr. Delamare s.n.* [non-type, NSW]).

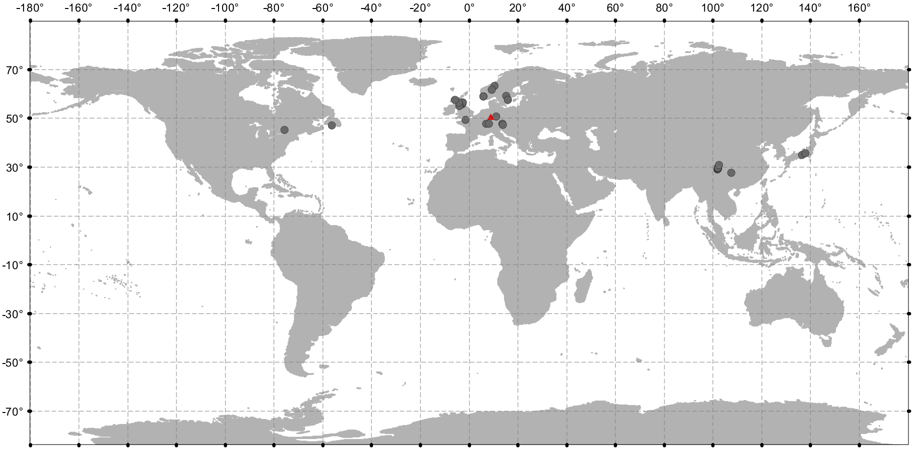


FIG. 87 – Distribution of *Ulota intermedia* worldwide. The red triangle indicates the type locality.

1889, *N. Bryhn s.n.* (NSW). TRØNDELAG: Trondheim, Ladehammeren, 11 Apr. 1896, *I. Hagen s.n.* (NSW).

Sweden. ÖLAND: Storebro, *R. Torf s.n.* (HBG). ÖSTERGÖTLAND: Vinnersta, s. date, *H. Holmgren s.n.* (H).

U.K. SCOTLAND: Arbroath, Nov. 1883, *W. Smith s.n.* (NSW), Oct. 1888, *s.n.* (NSW); Black Bank, New Galloways, Nov. 1884, *J. Mc Andrews s.n.* (NSW); East Lothian, 25 Apr. 1994, *D. G. Long 25309-2* (E); Gleu Abere, 1889, *R. C.* (NSW); Loch Torridon, 8 Sep. 1944, *W. Ross s.n.* (E); New Galloway, Nov. 1884, *J. Mc Andrew* (NSW); Perthshire, Killin, 17 Jul. 1885, *W. B. Waterfall* (NSW).

21. **ULOTA JAPONICA** (Sull. & Lesq.) Mitt., Trans. Linn. Soc. London, Bot. 3: 162. 1891. ≡ *Orthotrichum japonicum* Sull. & Lesq., Proc. Amer. Acad. Arts, 4: 277. 1859. TYPE: JAPAN. Hokkaido, Hakodadi, collected on trees shaded Hill sides during Com. Rogers N. Pacific Expl. Exp., Aug. 1859, *Charles Wright* (holotype, FH!).

Ulota nipponensis Besch., Ann. Sci. Nat., Bot., sér. 7, 17: 339. 1893. TYPE: JAPAN. Sanbongi, Mt. Ozore, *Faurie 11b* (lectotype, PC0101537! designated here; isolectotypes, BM000982382! KYO! S-B181066!); Sambongi, 6 Jun. 1886, *Faurie 554* (paratype, PC0101539–40!).

Plants 0.5–1 cm tall, yellow to green above, brown below. Stems usually branched. Leaves flexuose, sometimes moderately to strongly crisped when dry, patent when moist, (1.5–) 1.7–2.2 (–2.7) mm long, leaf lamina lanceolate, unistratose; leaf base slightly wide, rounded; apex acuminate; leaf margin plane, sometimes partially recurved; costa very strong, ending near the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (8–) 9–11 (–13) × (7–) 8–10 (–12) μm, thick-walled, with ca. 2 short papillae per cell on both surfaces; basal inner cells rectangular or elongate-rectangular, (14–) 24–36 (–51) × (4–) 6–9 (–12) μm, with slightly to moderately thickened wall, smooth; basal marginal cells often differentiated in (4–) 6–10 (–13) rows hyaline cells, quadrate to rectangular, with thickened transverse walls.

Autoicous. Perichaetial leaves somewhat longer, (2–) 2.2–2.8 (–3.1) mm. Vaginula naked. Seta (1.5–) 2–2.5 (–3) mm long, usually twisted when dry. Capsule short to long exserted, (1.3–) 1.5–2 mm long. Urn subglobose when moist, cylindrical to short-cylindrical when dry and empty, strongly constricted just below the mouth when dry, 8-ribbed the entire length. Neck short or long, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, often four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction of urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, united into 8 pairs, lanceolate, densely papillose throughout or striate near apex on the outside, striate throughout or papillose above and striate below on the inside, recurved when dry and often lying on the exothecium. Endostome segments 8, narrow-lanceolate, hyaline, uniseriate, 1/3–1/4 width of teeth in the middle part, smooth outside, slightly scabrous or finely papillose or nearly smooth inside, almost as long as teeth. Opercula with a short to medium-long beak. Calyptra mitrate, sparsely hairy or naked. Spores spherical, finely papillose, (16–) 19–22 (–25) μm in diameter.

Illustration: Noguchi and Iwatsuki (1989) and Wang and Jia (2012a); figures 88–90.

Habitat: It grows on branches or trunks of trees, such as *Pinus* and *Sorbus*. There are many records of altitude: (20–) 140–470 (–900) m. It is occasionally mixed with *Orthotrichum consobrinum*, *Ulota crispa*, and *U. drummondii*.

Distribution: It is common in Japan and occasionally in the Far East of Russia. Figure 91.

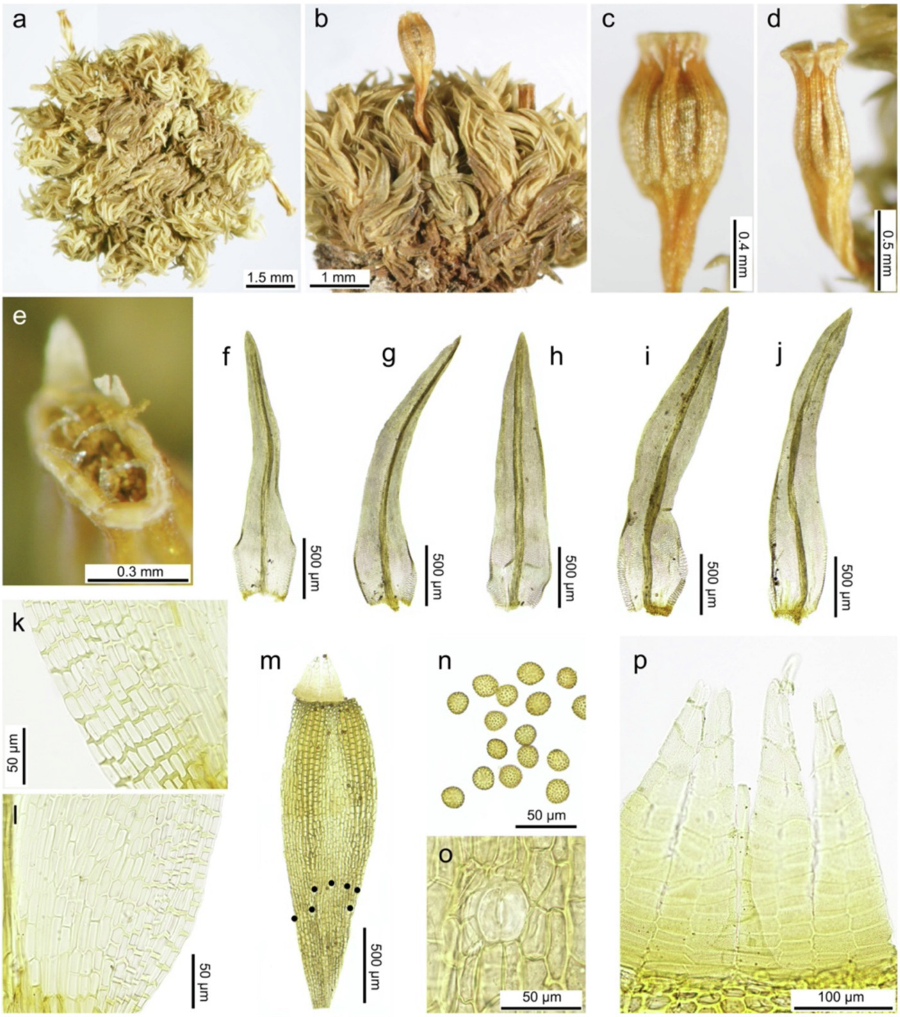


FIG. 88 – *Ulota japonica* (Sull. & Lesq.) Mitt. a–b. Habit. c–d. Capsules in dry. e. Capsule mouth viewed from above. f–h. Leaves. i–j. Perichaetial leaves. k–l. Marginal cells at leaf base. m. Exothecial wall, with dots indicating stoma position. n. Spores. o. Stoma. p. Peristome with a broken segment. (All from the holotype in FH).

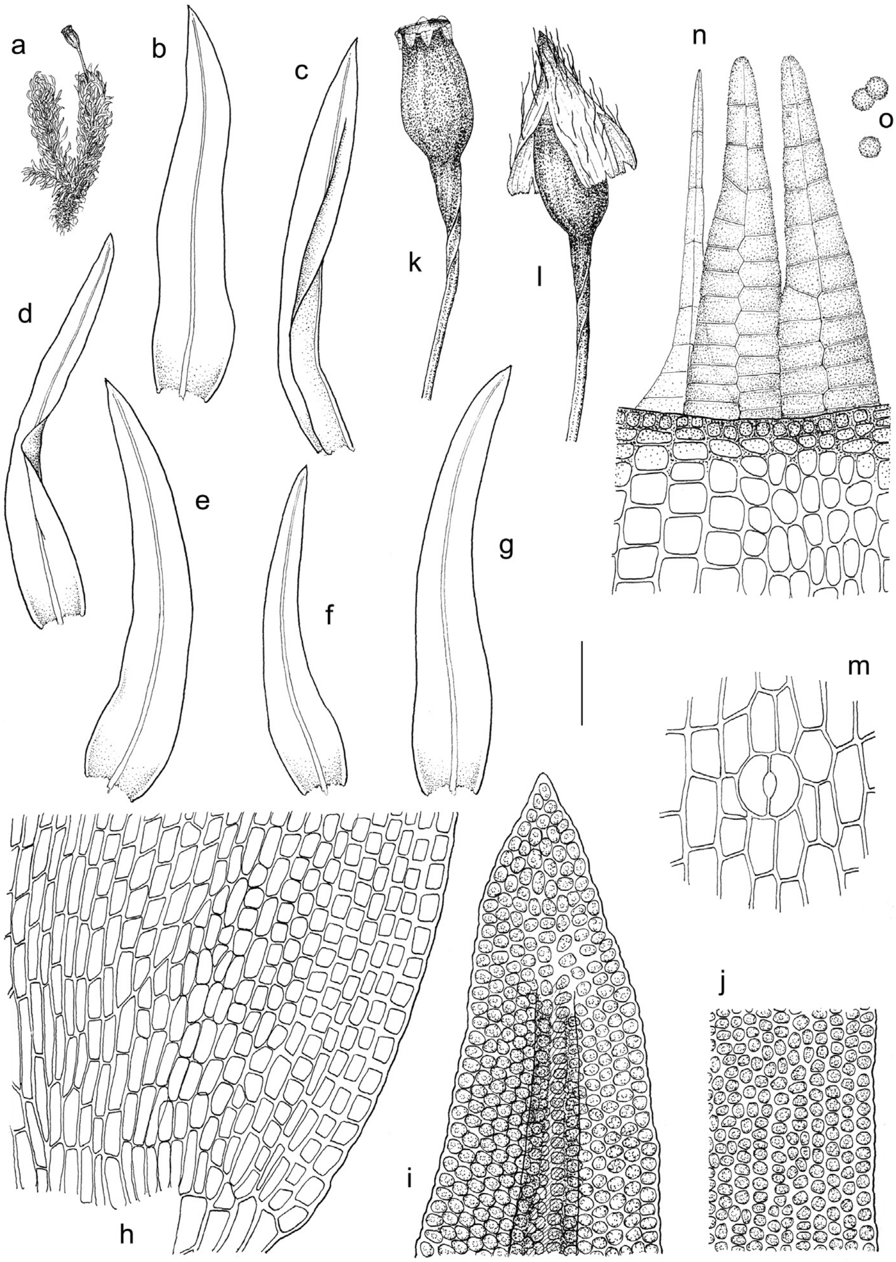


FIG. 89 – *Ulota japonica* (Sull. & Lesq.) Mitt. a. plant; b–d. leaves; e–g. perichaetial leaves; h. basal marginal cells; i. top laminal cells; j. median marginal cells; k. an empty capsule in dry; l. a capsule with calyptra; m. stoma; n. a portion of peristome; o. spores. (Scale bar: a, 5 mm; b–g, 0.48 mm; h–j and m, 0.05 mm; k–l, 3.33 mm; n–o, 0.07 mm. All drawn from holotype in FH except a, k and l from *Une* [non-type, HIRO]).

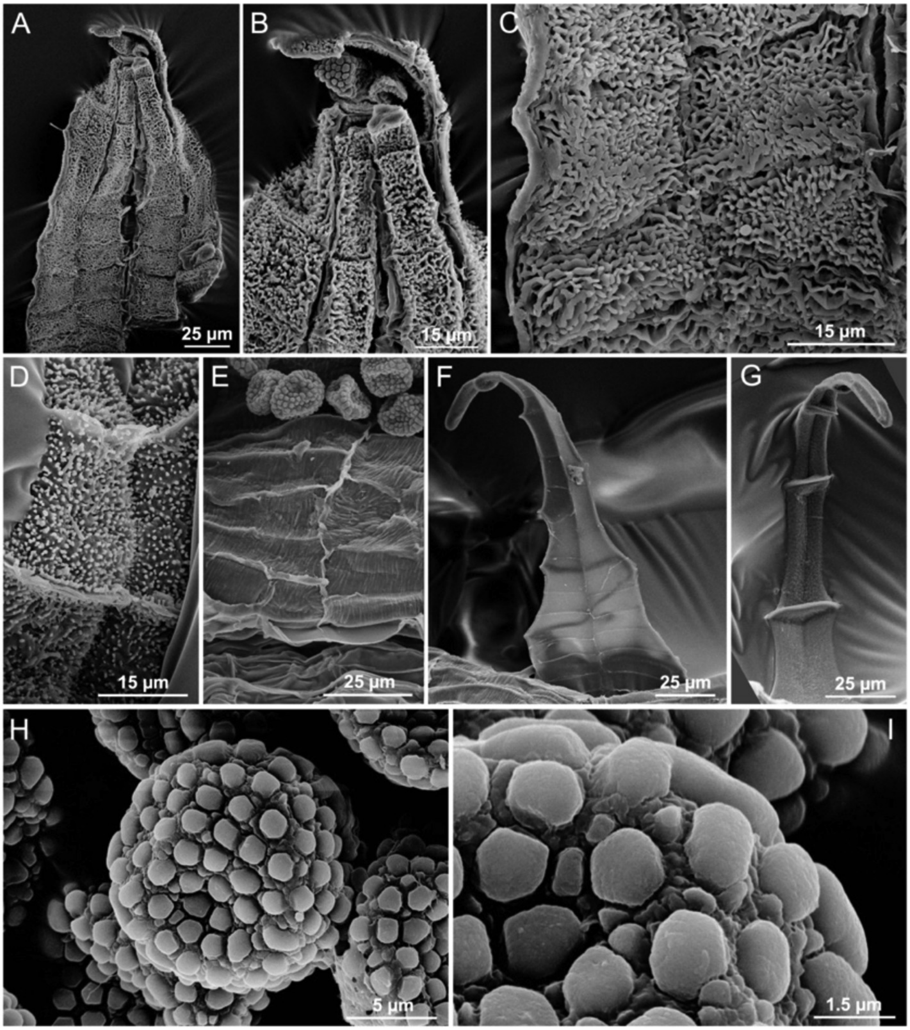


Fig. 90 – *Ulota japonica* (Sull. & Lesq.) Mitt. A, outer surface of exostome; B, outer surface of upper exostome; C, outer surface of basal exostome; D, inner surface of middle exostome; E, inner surface of basal exostome; F, outer surface of endostome; G, inner surface of endostome; H, spores; I, surface ornamentation of a spore. (All from the holotype in FH).

Notes: *Ulota japonica* is easily recognized by the small plant, often flexuose leaves with slightly wider base, cylindrical to short-cylindrical capsules, and nearly naked calyptra.

Ulota japonica resembles *U. perbreviseta* in the more or less short seta and the subglobose capsules when moist, but the latter differs in crisped leaves, less rows (4–6) of hyaline cells at basal leaf margins, emergent capsules that are not constricted when dry, densely hairy calyptra and larger spores (28–31 μm).

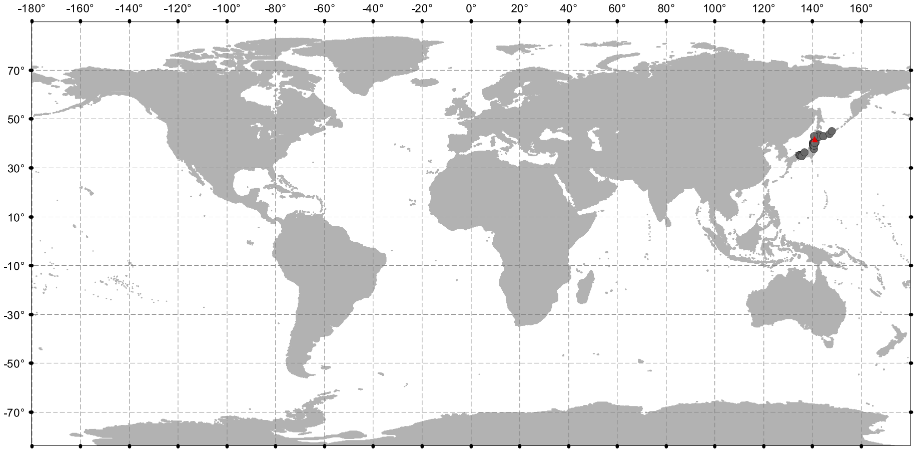


FIG. 91 – Distribution of *Ulota japonica* worldwide. The red triangle indicates the type locality.

Ulota japonica is also similar to *U. crispa* in conspicuously differentiated cells at basal leaf margins, cylindrical capsules that are strongly constricted when dry, and eight narrow endostome segments. However, *Ulota crispa* is distinguished by larger plants (0.5–2.5 cm), strongly crisped leaves with a distinctly wide base, leaf basal inner cells with strongly thickened walls, and densely hairy calyptra.

Key to *Ulota japonica* and its closely related species.

1. Capsules emergent, hardly constricted when dry; basal leaf margins have less rows (4–6) of hyaline cells; spores larger, 28–31 μm.............................. *U. perbreviseta*
1. Capsules short to long exserted, distinctly constricted when dry; basal leaf margins have more rows (5–11) of hyaline cells; spores relatively small, 19–25 μm..............................2
2. Leaves strongly crisped when dry, with distinctly wide base; leaf basal inner cells with strongly thickened wall; plants large, 0.5–2.5 cm; calyptra densely hairy.............................. *U. crispa*
2. Leaves often flexuose when dry, with slightly wide base; leaf basal inner cells with slightly to moderately thickened wall; plants small, 0.5–1 cm; calyptra sparsely hairy or naked.............................. *U. japonica*

Additional Specimens Examined: **Japan**. AKITA: 16 Jun. 1979, *Y. Takahashi YT-4316-2* (AKPM), 17 Jul. 1981, *YT-5804* (AKPM), 27 May 1984, *YT-7588* (AKPM), 23 Jun. 1985, *YT-8302* (AKPM), 10 May 2006, *YT-13432* (AKPM), 25 Jun. 2006, *YT-13533* (AKPM). AOMORI: Mt. Kinashi-dake, 9 Jul. 1978, *N. Saito 488* (TNS). FUKUSHIMA: Tamura, 23 Aug. 1994, *M. Higuchi 23472* (TNS). HOKKAIDO: Hidaka, Mt. Poroshiri, 27 Jul. 1971, *Z. Iwatsuki 518-1* (TNS); Kushiro Twp., 21 Sep. 2003, *W. B. Shofield 122407-2* (UBC), *122418-2* (UBC); s. loc., Jul. 1898, *Faurie 608* (PC). HYOGO: Ichijima-cho, 6 Mar. 2000, *H. Akiyama 14743* (HYO), *14749*

(HYO). ISHIKAWA: Kakuma-machi, 12 Nov. 1995, *H. Akiyama 13197* (HYO). OSAKA: Takatsuki-shi, 17 Mar. 2002, *M. Kimura 4427* (OSA); Toyono, 6 May 1956, *T. Nakazima 7175* (OSA). YAMAGATA: Hohsawa, 10 Nov. 1980, *Y. Sato 1* (TNS).

Russia. SAKHALIN: Iturup Island, 3 Aug. 2007, *V. A. Bakalin s.n.* (PE), 23 Aug. 2007, *s.n.* (PE).

22. **ULOTA LARRAINII** Garilleti, Mazimpaka & F. Lara, Phytotaxa 217(2): 133. 2015. TYPE: CHILE. Prov. Capitán Prat: Caleta Tortel, comienzo de "ruta turística", en tundras de *Donatia*, *Astelia* y *Lepidothamnus fonkii*, 47°47′32″ S, 73°31′48″ W, alt. ca. 90 m, epífito en *Nothofagus dombeyi*, 20 Ene [ro] 2007, *J. Larraín 26884A, con R. Vargas* (holotype, VAL-Briof; isotype, CONC).

Illustration: see Garilleti *et al.* (2015).

Description, habitat, and distribution: see Garilleti *et al.* (2015). Figure 92.

Notes: *Ulota larrainii* is a species recently published in South America (Garilleti *et al.*, 2015). It is characterized by multicellular spores according to the protologue. *Ulota larrainii* is very close to *Ulota billbuckii* in morphology. They both have non-crisped leaves, a few rows of hyaline cells at the basal leaf margin, 16 broad endostome segments, and multicellular spores.

According to Garilleti *et al.* (2015), their differences are that in *Ulota billbuckii* the eight paired exostome teeth completely split into 16 when dry, endostome segments have a remarkably tall continuous basal ring, and spores are oblong or irregularly elongate, while in *U. larrainii* exostome teeth keep in pairs when dry, endostome segments are free at the base and spores are mostly rounded in shape. However, only type specimens are cited in the protologue of *Ulota larrainii*, which indicates that the characters described are likely to have variations. Considering the quite detailed description and comparison in the protologue, we still accept it in this work. Due to neither type nor non-type specimens being seen by us, the characters of *Ulota larrainii* used in the key below are only based on the description in Garilleti *et al.* (2015).

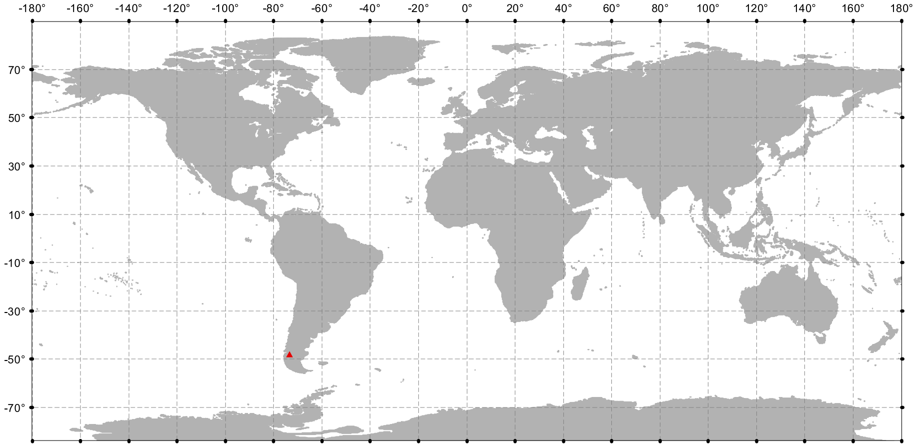


FIG. 92 – The type locality of *Ulota larrainii*.

Key to *Ulota larrainii* and its closely related species.

1. Spores unicellular, small, 36–44 μm..*U. magellanica*
1. Spores multicellular, large, 85–140 μm..2
2. Endostome segments remarkably connected by some cells at lower half part...*U. billbuckii*
2. Endostome segments almost free at the base..................................*U. larrainii*

Additional Specimens Examined: None.

23. **Ulota laticiliata** Malta, Acta Horti Bot. Univ. Latv. 7: 11. 1933. Type: Australia. Tasmania, S. E. Coast, Recherche Bay, "Moss Glen", near Ramsgate, on apple trees, at sea level, 17 Jan. 1911, *W. A. Weymouth 2487* (lectotype, H4336012! designated by Ramsay, 2006; isolectotype, HO71749!); Tasmania, Mt. Wellington, 6 Mar. 1891, *W. A. Weymouth 227* (paralectotype, H; isoparalectotype, HO).

Plants 0.5–1.5 cm tall, yellow above, brown below. Stems usually branched. Leaves strongly crisped when dry, erect-patent to patent when moist, (1.6–) 2–2.2 (–2.5) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex acuminate; leaf margin plane or rarely partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, oblong, (5–) 6–8 (–11) × (5–) 7–10 (–11) μm, thick-walled, with 1–3 low simple papillae per cell, occasionally almost smooth; basal inner cells linear to elongate-rectangular, (17–) 29–42 (–60) × (2–) 3 (–4) μm, with strongly thickened wall, smooth; basal marginal cells distinctly differentiated, (3–) 4–10 (–13) rows, hyaline, quadrate to rectangular, with transverse walls moderately to strongly thickened.

Autoicous. Perichaetial leaves are somewhat longer, 2.3–2.5 (–2.8) mm. Vaginula naked. Seta (3–) 4.5–6 (–7.2) mm long, twisted anticlockwise when dry. Capsule long exserted, 1.2–1.5 mm long. Urn cylindrical to long-cylindrical strongly constricted below the mouth when dry and empty, eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, usually four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, variably recurved when dry, sometimes lying on the exothecium, lanceolate, densely and finely papillose on the outside, striate-papillose below, and papillose above on the inside. Endostome segments 8, lanceolate, almost as tall as teeth, uniseriate to partially biseriate, about 1/2 width of teeth in the middle, hyaline, smooth outside, finely papillose or slightly coarse inside. Opercula with a short beak. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (18–) 24–28 (–33) μm in diameter.

Illustration: Malta (1933) and Sainsbury (1955); figures 93 and 94.

Habitat: It grows on trunks or branches of trees or shrubs, rarely on rock. It is often epiphytic on *Acacia*, *Atherosperma*, *Dacrydium*, *Melicytus*, *Nothofagus*, and

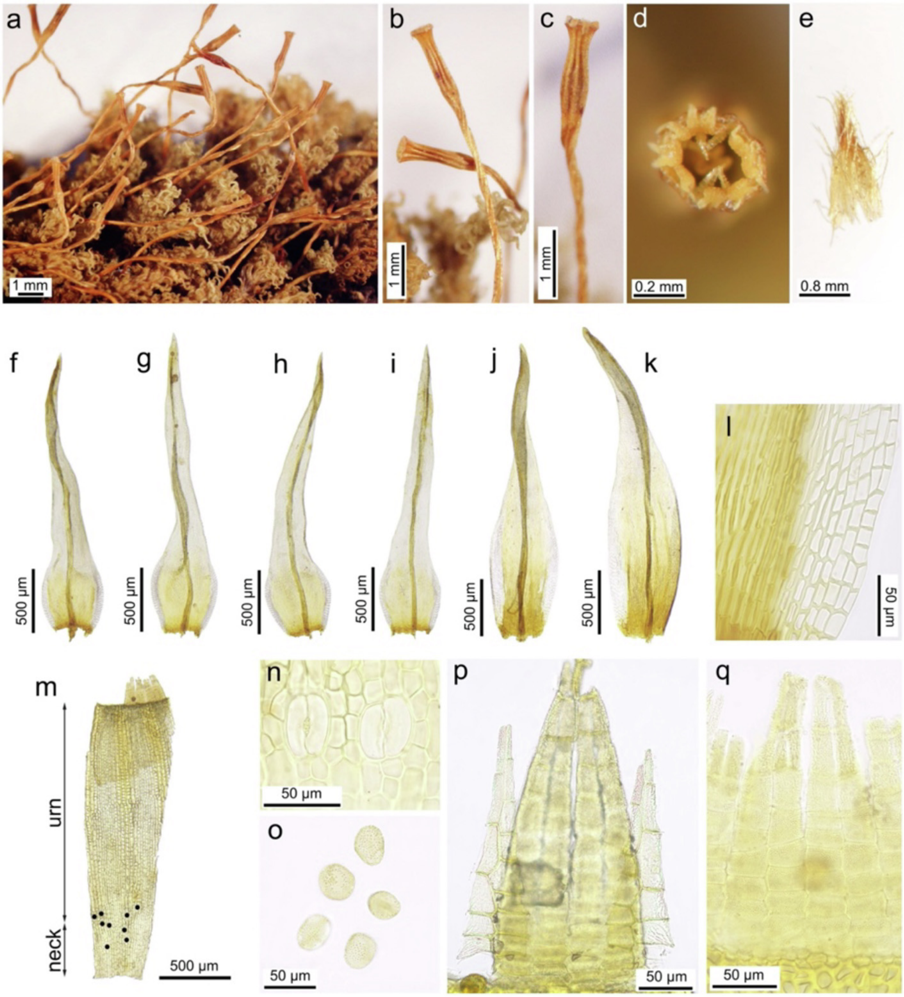


FIG. 93 – *Ulota laticiliata* Malta. a. Habit. b–c. Capsules in dry and empty. d. Capsule mouth viewed from above. e. Calyptra. f–i. Leaves. j–k. Perichaetial leaves. l. Marginal cells at leaf base. m. Exothecial wall, with dots indicating stoma position. n. Stomata. o. Spores. p. Peristome inside view. q. Peristome outside view. (All from the isolectotype in HO, except a–c from *J. K. Bartlett s.n.* [non-type, AK], d–e from the syntype in H and p from *A. J. Fife 11519* [non-type, CHR]).

Olearia. There are many records of altitude: (6–) 600–1195 (–1371) m. It occasionally grows with *Orthotrichum tasmanicum*, *Ulota cochleata*, and *U. viridis*.

Distribution: It is common in Tasmania (Australia) and New Zealand. Figure 95.

Notes: *Ulota laticiliata* is characteristic of the strongly crisped leaves, many rows of hyaline cells at basal leaf margins, and broader endostome segments.

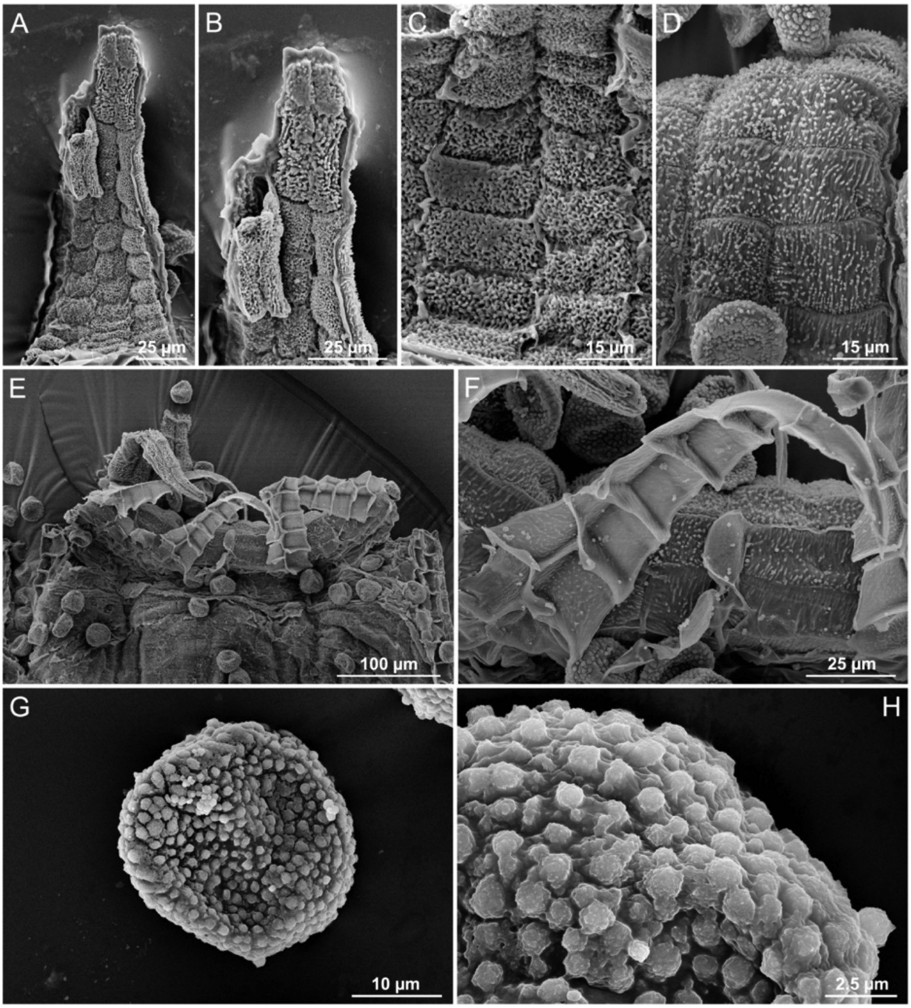


FIG. 94 – *Ulota laticiliata* Malta. A, outer surface of exostome; B, outer surface of upper exostome; C, outer surface of basal exostome; D, inner surface of middle exostome; E, endostome segments; F, inner surface of endostome; G, a spore; H, surface ornamentation of a spore. (All from the lectotype in H except B from the isolectotype in HO).

Fife (1995; 2004 in herb.) placed *Ulota laticiliata* into the synonymy of *U. lutea* (synonymized with *Ulota crispa* by us in 2012b) based on the New Zealand materials. As Malta (1933) mentioned, *Ulota laticiliata* is indeed closely related to *U. lutea*, but differs in the wider endostome segments. In addition, Ramsay (2006) suggested that there were differences between *Ulota laticiliata* and *U. lutea* besides the endostome segments. For example, the leaves in *Ulota laticiliata* are gradually narrowed from the bases, and have more rows of hyaline cells at basal leaf margins

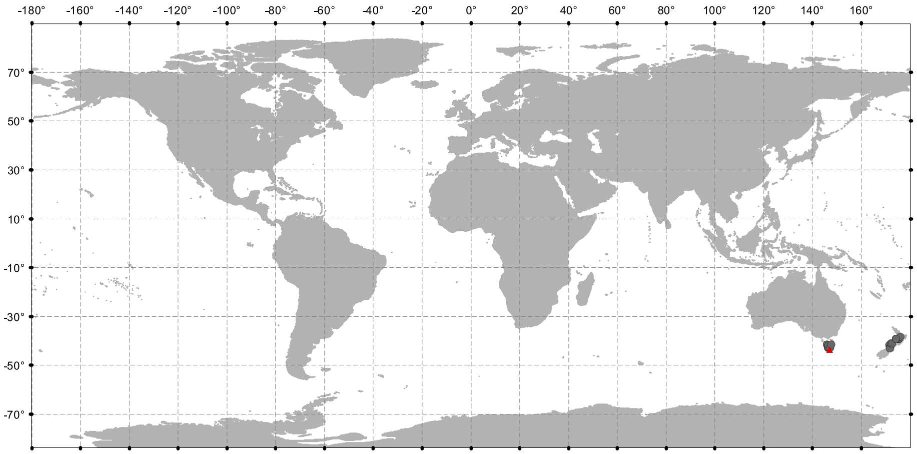


Fig. 95 – Distribution of *Ulota laticiliata* worldwide. The red triangle indicates the type locality.

(*vs.* 2–5 rows in the local *U. crispa*). Our study confirms Ramsay's view (2006), and we thus regard *Ulota laticiliata* as a separate species here.

In terms of endostome segments, *Ulota laticiliata* is similar to *U. obtusiuscula* from North America. Besides that, both also have strongly crisped leaves, distinctly differentiated cells at basal leaf margins, very long seta, and densely hairy calyptra. But *Ulota obtusiuscula* differs in the larger plants (2–2.5 cm), and the capsules often with a long neck and hardly constricted when dry.

No noteworthy variation was observed in *Ulota laticiliata*.

Key to *Ulota laticiliata* and its closely related species.

1. Capsules with long neck, hardly constricted when dry; exothecial cells near mouth sometimes red or orange; plants larger, 1–3.5 cm............ *U. obtusiuscula*
1. Capsules with short neck, strongly constricted when dry; exothecial cells near mouth never red or orange; plants relatively small, 0.5–1.5 cm........................2
2. Hyaline cells at basal leaf margins differentiated in less rows, 2–5 rows; endostome segments linear to narrow-lanceolate, 1/3–1/4 width of teeth in the middle.. *U. crispa* (locally)
2. Hyaline cells at basal leaf margins differentiated in more rows, 4–10 rows; endostome segments lanceolate, about 1/2 width of teeth in the middle.. *U. laticiliata*

Additional Specimens Examined: **Australia**. Tasmania: Boyd Lookout, 16 Feb. 2000, *J. Jarman s.n.-1* (HO); Central Highlands, Mother Cummings Peack, 20 Feb. 1986, *A. Moscal 12339A* (HO); Corinna Road, 12 May 1997, *H. Streimann 59711* (H); Creek, Watchorn's Hill, 1 Jan. 1890, *W. A. Weymouth 1540* (HO); Mt. Lord, 30 Jan. 1993, *J. Jarman s.n.* (HO); Mt. Saddleback, 14 Aug. 1993, *J. Jarman s.n.-2* (HO); Vale of Belvoir, 13 Mar. 2010, *L. H. Cave 1084* (HO).

New Zealand. Canterbury: Arthur's Pass National Park, 1 Feb. 1984, *A. J. Fife 6165* (MICH). Manawatu-Wanganui: Taumarunui Co., 25 Nov. 2013, *P. J. de Lange 11762* (AM), 14 Aug. 1978, *J. K. Bartlett s.n.* (AM). Taranaki: Egmont National Park, 28 Nov. 2001, *J. E. Braggins s.n.* (AM), Dec. 1978, *J. K. Bartlett s.n.* (AM), 15 Jan. 1935, *G. O. K. Sainsbury* (S), *1571/35* (MICH). Tasman: Cobb Valley, 4 Jun. 1989, *B. Polly s.n.* (AM); Golden Bay Co., *J. K. Bartlett s.n.* (AM). Waikato: prope Atiamuri, 4 May 1931, *K. W. Allison 22* (S). West Coast: Buller Co., May 1979, *J. K. Bartlett s.n.* (AM).

24. **Ulota latisegmenta** Q.H. Wang & Y. Jia, Bryologist 115(3): 429. 2012. Type: China. Sichuan, Emei mountain, near Jinding, on trunk, 25 Aug. 1942, *P.-C. Chen 5596* (holotype, PE!).

Plants 1–2 cm high, green on the top, brown to black below. Stems usually branched. Leaves moderately to strongly crisped when dry, patent when moist, (3–) 3.3–3.5 (–3.8) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex long acuminate; leaf margin plane or partially recurved; costae strong, ending near the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (5–) 9–12 (–15) × (7–) 8–11 (–13) μm, thick-walled, with 1–2 low simple papillae per cell; basal inner cells rhomboidal, linear, rectangular and elongate-rectangular, (17–) 22–27 (–33) × (5–) 6–8 (–10) μm, smooth, thick-walled; basal marginal cells weakly differentiated in (1–) 2–4 (–5) rows, hyaline, quadrate to rectangular, with only transverse walls moderately to strongly thickened.

Autoicous. Perichaetial leaves are somewhat longer, 3.7–4.3 mm. Vaginula is sparsely hairy or naked. Seta (3–) 4–5.4 (–7) mm long, twisted anticlockwise when dry. Capsules short to long exserted, (1.7–) 2–2.6 (–3) mm long. Urn short- to long-cylindrical, strongly or sometimes slightly constricted when empty and dry, 8-ribbed along the entire length. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, usually four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction of urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, united into 8 pairs, often recurved and lying on the exothecium when dry, lanceolate, strongly and densely papillose on the outside, papillose to papillose-striate on the inside. Endostome segments 16, 8 long 8 short (short ones sometimes caducous), lanceolate, united by some cells at the lower part, partially biseriate or uniseriate, ≥1/2 width of teeth at the middle part, hyaline or pale yellow, smooth outside, finely papillose inside. Opercula with a short to medium-long beak. Calyptrae mitrate, moderately to strongly densely hairy. Spores globose, finely papillose, (16–) 19–25 (–33) μm diameter.

Illustration: Wang and Jia (2012a); figures 96 and 97.

Habitat: It grows on trunks or branches of trees, such as *Abies*. There are some records of altitude: 1600–3000 m. It occasionally grows with *Ulota delicata* and *Orthotrichum jetteae*.

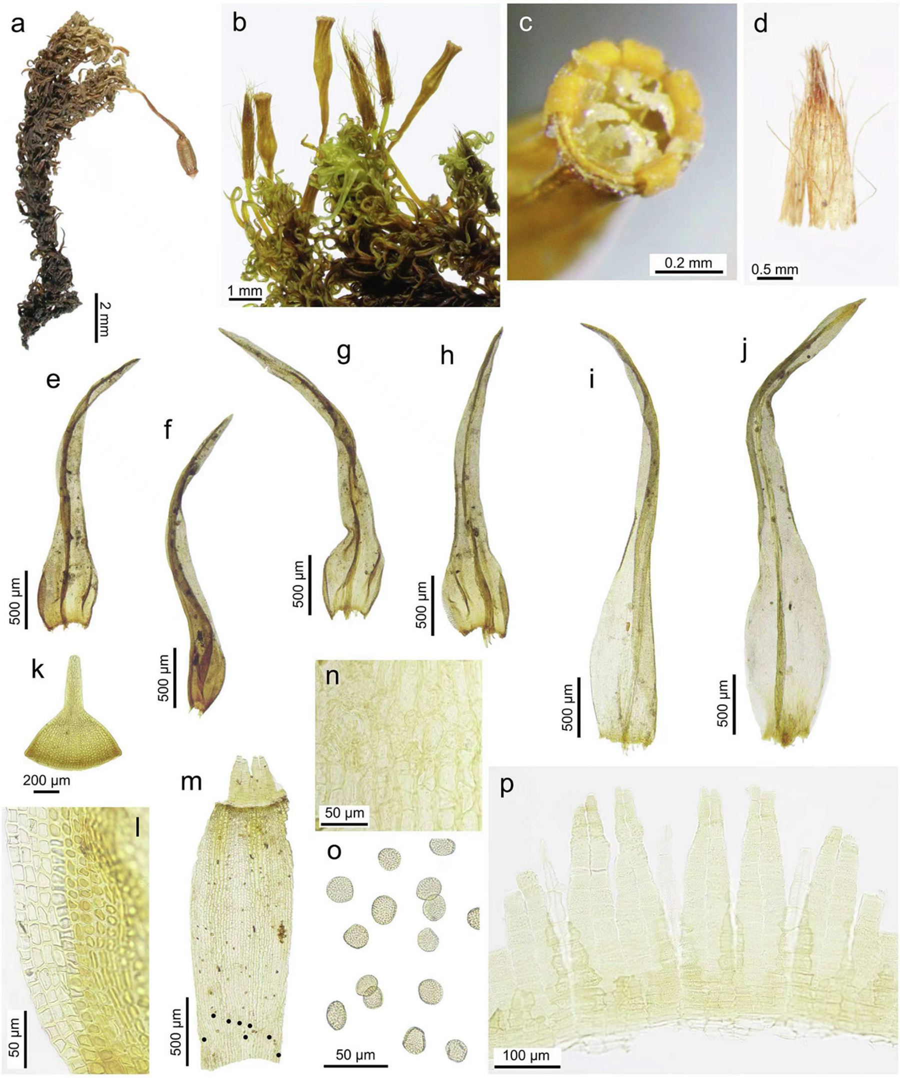


FIG. 96 – *Ulota latisegmenta* Q.H. Wang & Y. Jia. a. Habit. b. Capsules in dry. c. Capsule mouth viewed from above. d. Calyptra. e–h. Leaves. i–j. Perichaetial leaves. k. Operculum. l. Marginal cells at leaf base. m. Exothecial wall, with dots indicating stoma position. n. Stomata. o. Spores. p. Peristome. (All from the holotype in PE except b–c from *Y. Jia and L. Luo 20597* [non-type, PE]).

Distribution: It is **endemic** to China. Figure 98.

Notes: *Ulota latisegmenta* is characterized by crisped leaves, weakly differentiated cells at basal leaf margins, constricted capsules, and 16 wide endostome segments.

Its wide endostome segments remind us of *Ulota robusta* in the Himalaya region. They also share a few rows of hyaline cells at basal leaf margins. However, *Ulota*

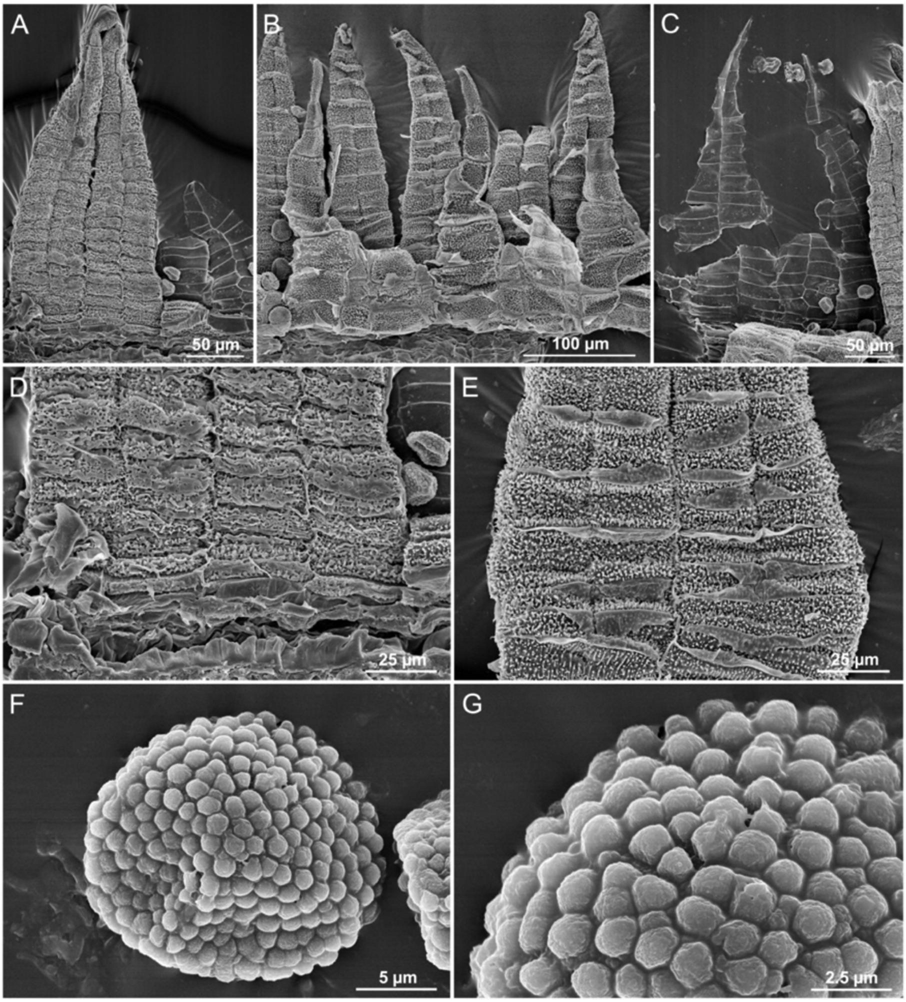


FIG. 97 – *Ulota latisegmenta* Q.H. Wang & Y. Jia. A, outer surface of exostome; B, inner surface of exostome and endostome; C, outer surface of endostome; D, outer surface of basal exostome; E, inner surface of middle exostome; F, spores; G, surface ornamentation of a spore. (All from the holotype in PE).

robusta differs in hardly constricted capsules, striate endostome segments, larger plants (1–4 cm), and larger spores (32–37 μm). Besides, *Ulota latisegmenta* also apparently looks like *U. crispa*, both having crisped leaves and long exserted cylindrical capsules, but in the latter, there are more rows (5–11) of hyaline cells at basal leaf margins and narrow-lanceolate endostome segments.

Through more specimens studied, we found that *Ulota latisegmenta* has some variation in leaf crispness, capsule shape, and contraction degree of capsules.

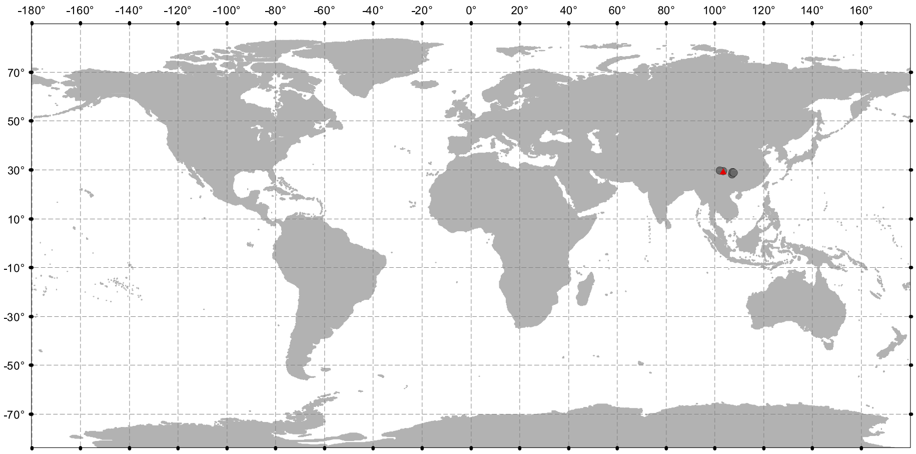


FIG. 98 – Distribution of *Ulota latisegmenta* worldwide. The red triangle indicates the type locality.

This causes its relationship with *Ulota robusta* a little obscure, and we are trying to solve it by molecular methods. For more discussion, see Notes in *Ulota robusta*.

Key to *Ulota latisegmenta* and its closely related species.

1. Endostome segments narrow; hyaline cells at basal leaf margins in more rows (5–11).. *U. crispa*
1. Endostome segments wide; hyaline cells at basal leaf margins in few rows (2–4).. 2
2. Endostome segments striate; capsules hardly constricted; plants larger, 1–4 cm; spores larger, 32–37 μm.. *U. robusta*
2. Endostome segments finely papillose; capsules often strongly constricted; plants smaller, 1–2 cm; spores smaller, 19–25 μm.. *U. latisegmenta*

Additional specimens examined (all in PE unless otherwise noted): **China**. CHONGQING: Nanchuan, Jinfo Mt., 29 Jul. 1986, *M.-Z. Wang 860047*, Aug. 1945, *Y. Chen 3*, 9 Apr. 1935, *P.-C. Chen 1680*, 20 Aug. 1987, *X.-Y. Hu H0721a*. GUIZHOU: Daozhen Co., Mopancun, 7 Aug. 2003, *Y.-Q. Huang 449*; Zunyi, Tongzi Co., 15 Jul. 2016, *s. coll.* SICHUAN: Emei Mt., Jinding, 25 Aug. 1942, *P.-C. Chen 5584*, *5596*, *5619b-2*, 2 Aug. 1980, *Q. Li 5169* (IFP); Leshan, Mabian Co., Dafengding Nature Reserve, 7 Jul. 2012, *Q. He H5330.*

25. **ULOTA LUTEOLA** (Hook. f. & Wilson) Wijk & Margad., Taxon 10: 26. 1961. ≡ *Orthotrichum luteolum* Hook.f. & Wilson, Fl. Antarctica 2: 403. 1847. TYPE: CHILE. Tierra del Fuego, "Hermite Island, Cape Horn.", 1839–1843, *J. D. Hooker 141b* (syntypes, BM, lost in mail); "South part of Tierra del Fuego, *C. Darwin, Esq., n. 440*" (syntypes, BM, lost in mail).

Ulota fulvella Mitt., J. Proc. Linn. Soc. 4: 75. 1860. ≡ *Orthotrichum fulvellum* (Mitt.) Mitt., J. Linn. Soc., Bot. 12: 191. 1869. *Illegitimate, type of earlier name included.* Type: Chile. Tierra del Fuego, "Hermite Island, Cape Horn.", 1839–1843, *J. D. Hooker s.n.* (holotype, NY; isotype, H2057001!).

Ulota immarginata Cardot, Bull. Herb. Boissier, sér. 2, 5: 1004. 1905. Type: Argentina. "Terre-de-Feu: Ushuaia, ad trunc. *Nothofagi antarcticae*, 25 Sep. 1902, *C. Skottsberg 91*" (holotype, PC0703850! isotype, S-B158028!). Proposed by Malta (1927) as a synonym of *U. pygmaeothecia.*

Ulota pygmaeothecia (Müll. Hal.) Kindb., Enum. Bryin. Exot. 79. 1888. ≡ *Orthotrichum pygmaeothecium* Müll. Hal., Flora 68: 418. 1885. Type: Chile. Fuegia, ad ramos *Maytheni magellanicae* montls Darwin 1882, *Spegazzini* (lectotype, H4334012! designated by Wang and Jia, 2016, isolectotype, PC0101543!). Proposed by Wang and Jia (2016).

Ulota savatieri Besch., Bull. Soc. Bot. France 32: LXII. 1885. Type: Chile. Patagonie occidentale, Wellington island, Port Edén, 24 Feb. 1877, *Dr. Savatier* (holotype, PC0108134! PC0099349–50! isotype, BM000879988!). Proposed by Malta (1927) as a synonym of *U. fulvella.*

Plants 0.5–2.0 cm high, yellow to green on the top, brown to black below. Stems usually branched. Leaves erect to flexuose, sometimes slightly crisped when dry, erect-spreading when moist, (1.1–) 1.6–2.2 (–2.5) mm long; leaf lamina lanceolate, unistratose; leaf base wide, ovate to rounded; apex acute, acuminate to long acuminate; leaf margin plane or partially recurved; costae strong, ending near the apex. Upper and middle laminal cells irregularly rounded to oblong, (8–) 10–13 (–15) × (6–) 8–9 (–12) μm, thick-walled, with 1–2 low papillae per cell; basal inner cells linear, rectangular to elongate-rectangular, (20–) 24–30 (–38) × (3–) 5–6 (–8) μm, smooth, strongly thick-walled; basal marginal cells weakly differentiated in 1–3 rows, hyaline, quadrate to rectangular, with equally slightly thickened walls or somewhat thickened transversely walls.

Autoicous. Perichaetial leaves are somewhat longer, (2.0–) 2.2–2.5 (–2.6) mm long. Vaginula is naked or rarely hairy. Seta (1.5–) 3–4.5 (–8) mm long, twisted anticlockwise when dry. Capsules long exserted, (1.2–) 1.4–1.8 mm long. Urn cylindrical, strongly constricted when empty and dry, 8-ribbed along the entire length. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, usually four to five cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the base of the urn or the transition zone between the urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, united into 8 pairs, often recurved and lying on the exothecium when dry, lanceolate, densely papillose on the outside, papillose to striate-papillose on the inside. Endostome segments 8, linear to narrow-lanceolate, biseriate or uniseriate, 1/3–1/4 width of teeth at the middle part, yellowish or hyaline, smooth outside, smooth or slightly scabrous on the inside. Opercula with a short to medium-long beak. Calyptrae mitrate, densely hairy. Spores globose, finely papillose, (26–) 29–34 (–40) μm diameter.

Illustration: Malta (1927) and Muñoz-Puelles *et al.* (2017); figures 99–104.

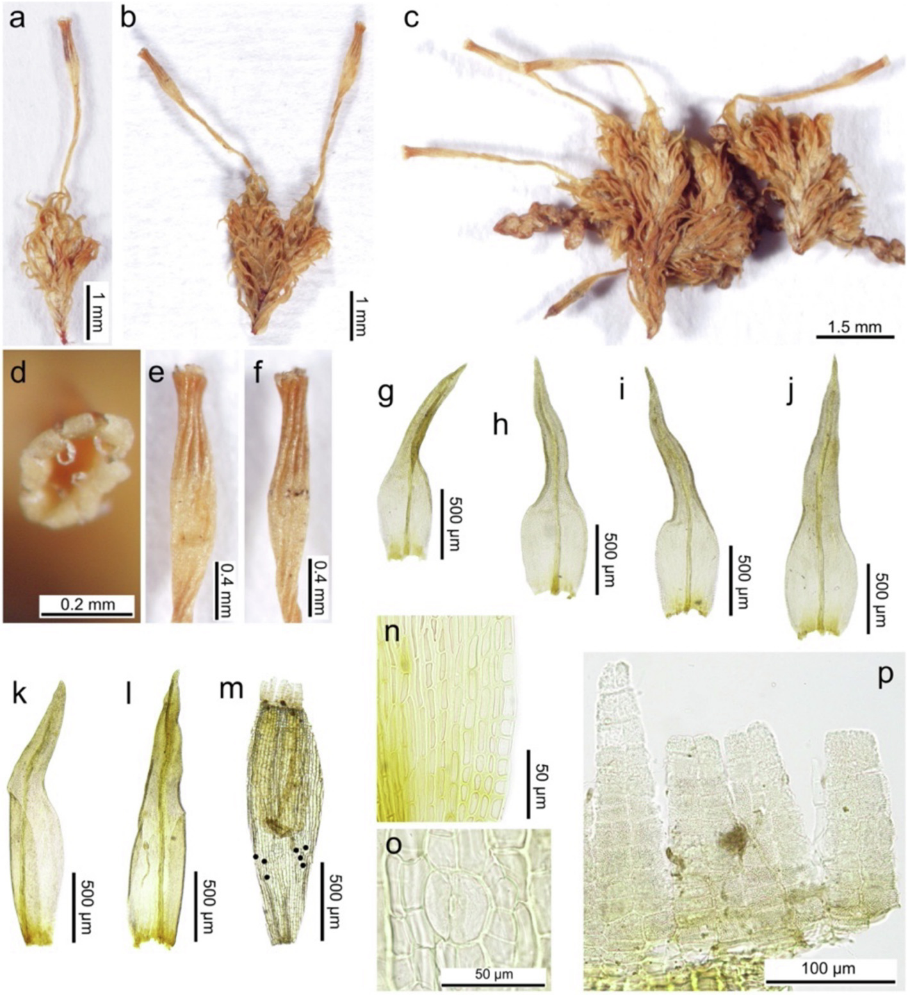


Fig. 99 – *Ulota luteola* (Hook. f. & Wilson) Wijk & Margad. a–c. Habit. d. Capsule mouth viewed from above. e–f. Capsules in dry and empty. g–j. Leaves. k–l. Perichaetial leaves. m. Exothecial wall, with dots indicating stoma position. n. Marginal cells at leaf base. o. Stoma. p. Peristome with most incomplete. (All from the isolectotype of *U. pygmaeothecia* in PC).

Habitat: It is common on shrubs or trees, as reported by Muñoz-Puelles *et al.* (2017), which is confirmed by the only record in this study. Its altitude is also only one record, at 150 m.

Distribution: It occurs in the southern part of Chile and Argentina. Figure 105.

Notes: *Ulota pygmaeothecia* was recently reduced in the synonymy with *U. luteola* (Wang and Jia, 2016), but was soon reinstated by Muñoz-Puelles *et al.* (2017). They listed some morphological differences between them in which the significant distinction based on our study is the leaf shape, as well as seta length and

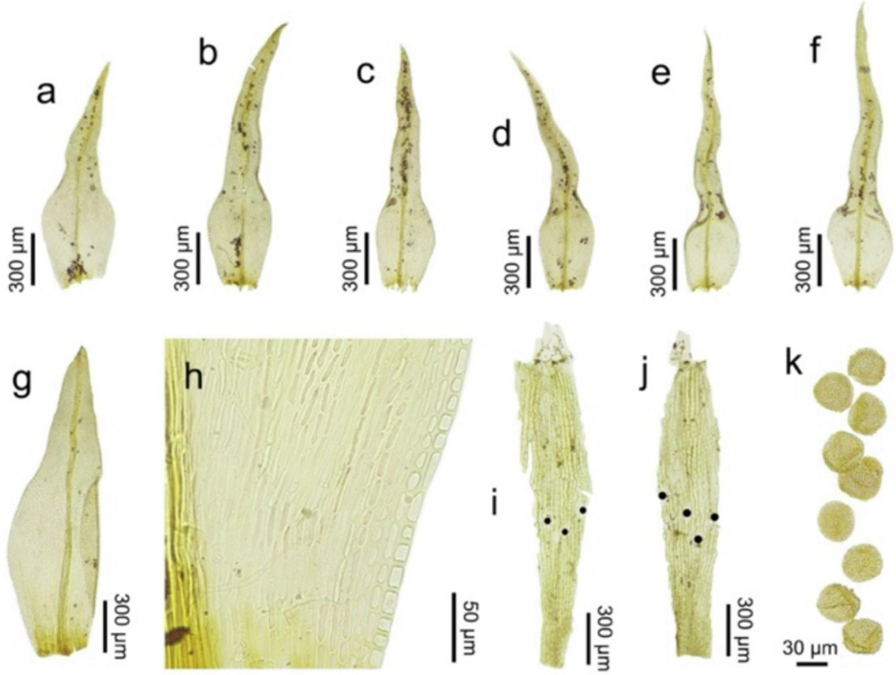


FIG. 100 – *Ulota luteola* (Hook. f. & Wilson) Wijk & Margad. a–f. Leaves. g. Perichaetial leaf. h. Marginal cells at leaf base. i and j. Exothecial wall, with dots indicating stoma position. k. Spores. (All from *P. Dusén s.n.* [non-type, H]).

spore size. The leaf shape in *Ulota pygmaeothecia* and *U. luteola* varies considerably, from acute to long acuminate at the apex and from ovate to rounded at the base (figures 99 and 104). This was also indicated in Malta's illustration of *Ulota pygmaeothecia* (1927). However, our current study suggests that this variation seems to be continuous, while *Ulota pygmaeothecia* and *U. luteola* are only two extremes of variation (figures 99–104). At the same time, the seta length does not change regularly with the variation of leaf shape, although the spore, to some extent, changes from large to small with the leaf apex from acute to long acuminate. Therefore, we still consider *Ulota pygmaeothecia* as conspecific with *U. luteola* before more evidence is found, such as molecular data.

The diagnostic characteristics for *Ulota luteola* are erect to flexuose leaves, hardly differentiated leaf cells at basal margins, cylindrical capsules that are strongly constricted when dry and empty, eight narrow endostome segments, and densely hairy calyptra. It was also reported from New Zealand by Sainsbury (as *Ulota pygmaeothecia*, 1945 and 1955), which was recently considered a misidentification and excluded from the flora of New Zealand (Wang and Jia, 2018a; Muñoz-Puelles *et al.*, 2017).

Locally, *Ulota luteola* resembles *U. pycnophylla* most, both having non-crisped leaves, strongly constricted cylindrical capsules, eight narrow endostome segments,

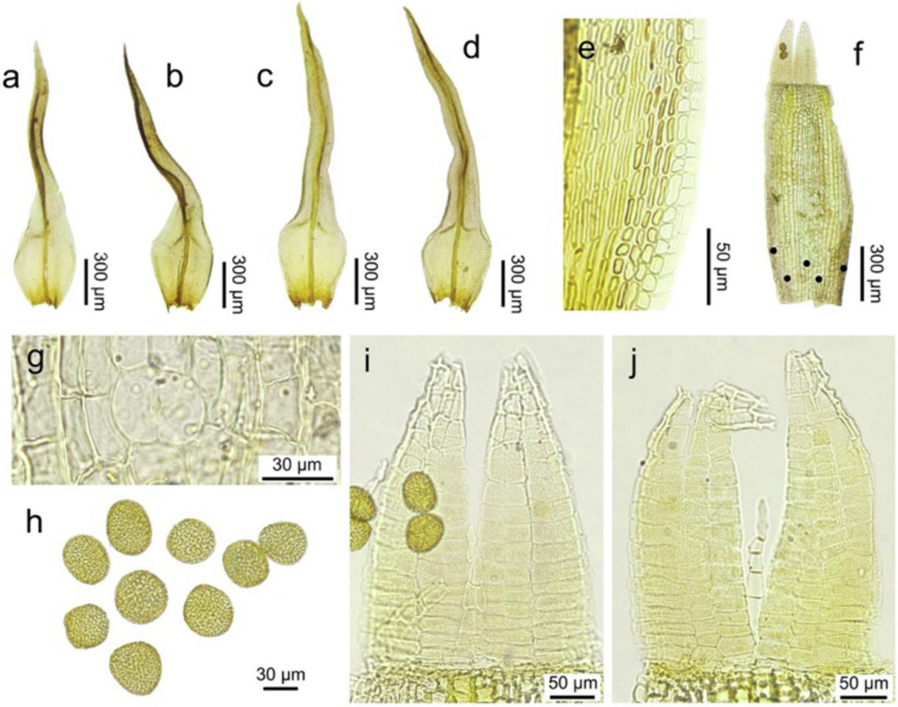


FIG. 101 – *Ulota luteola* (Hook. f. & Wilson) Wijk & Margad. a–d. Leaves. e. Marginal cells at leaf base. f. Exothecial wall, with dots indicating stoma position. g. Stoma. h. Spores. i–j. Peristome. (All from *R. Thaxter 167* [non-type, PC]).

and densely hairy calyptra. But *Ulota pycnophylla* can be separated by the many rows (5–10) of hyaline thin-walled cells at basal leaf margins and the always small leaves (1.1–1.5 mm).

Outside South America, *Ulota luteola*, with non-crisped leaves, hardly differentiated leaf cells at basal margins, cylindrical capsules, and eight narrow endostome segments, is similar to some species from North Hemisphere, such as *U. curvifolia*, *U. megalospora*, and *U. reptans*. However, *Ulota curvifolia* differs in the relatively larger plants (2–4 cm), high papillose on upper leaf cells, prominently striolate on exostome teeth and saxicolous growth, *U. megalospora* differs in often weakly constricted capsules with long neck, smaller leaves (1.2–1.7 mm), larger spores (41–51 μm) and often sparsely hairy calyptra, while *U. reptans* can be distinguished by the smaller leaves (1.3–1.6 mm), capsules hardly constricted when dry and often sparsely hairy calyptra. Moreover, *Ulota luteola* is also close to both-hemisphere distributed *U. crispa*. Their sporophytes are quite similar, having constricted cylindrical capsules, stomata often restricted to the junction of urn and neck, eight narrow endostome segments and hairy calyptra. However, *Ulota crispa* can be distinguished by the strongly crisped leaves and many rows (5–11) of hyaline cells at basal leaf margins.

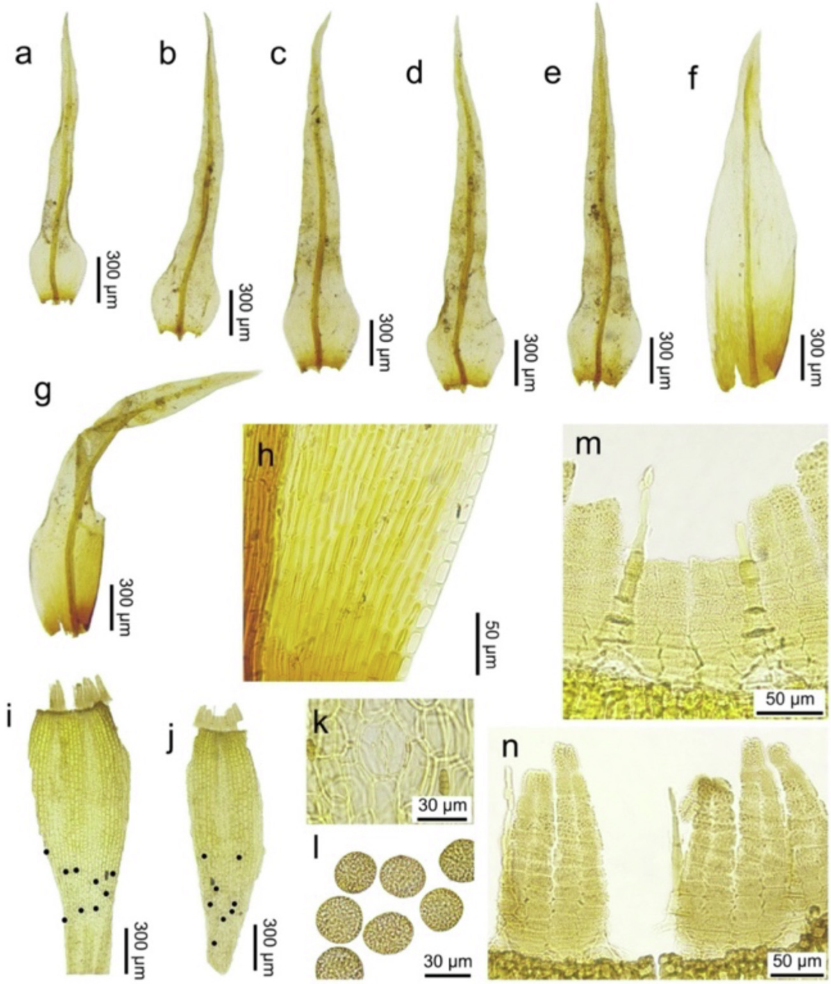


FIG. 102 – *Ulota luteola* (Hook. f. & Wilson) Wijk & Margad. a–e. Leaves. f–g. Perichaetial leaves. h. Marginal cells at leaf base. i–j. Exothecial wall, with dots indicating stoma position. k. Stoma. l. Spores. m–n. Peristome. (All from *H. Roivainen s.n.* [non-type, H]).

The leaf in *Ulota luteola* varies greatly from shape to size, as mentioned above.

Key to *Ulota luteola* and its closely related species.
1. Leaves strongly crisped when dry..*U. crispa*
1. Leaves erect to flexuose, rarely crisped when dry..2
2. Leaf cells at basal margins distinctly differentiated, 5–10 rows, with thin wall..*U. pycnophylla*

2. Leaf cells at basal margins weakly differentiated, often no more than 3 rows, with thin or only thickened transverse walls..3
3. Upper and middle leaf cells often with prominent conic or forked papillose; exostome teeth with strongly striolate; plants large, usually 2–4 cm high; often saxicolous growth..*U. curvifolia*
3. Upper and middle leaf cells often with low simple papillose; exostome teeth with densely papillose or striate-papillose; plants relatively small, usually no more than 2 cm high; epiphytic growth...4
4. Capsules strongly constricted when dry and empty; leaves relatively larger, 1.6–2.2 mm; calyptra densely hairy..*U. luteola*
4. Capsules hardly, sometimes distinctly constricted when dry and empty; leaves smaller, 1.2–1.7 mm; calyptra often sparsely hairy..5
5. Capsules with long neck when dry and empty, which makes the stomata apparently at the central part of capsules; spores larger, 41–51 μm; seta longer, 3–4.5 mm..*U. megalospora*
5. Capsules with short neck when dry and empty and the stomata located at the base of urn or the junction between urn and neck; spores smaller, 30–38 μm; seta shorter, 2.5–3.2 mm..*U. reptans*

Additional Specimens Examined: **Argentina**. TIERRA DEL FUEGO: Ushuaia, 8 Mar. 1903, *M. S. Pennington 349* (S); s. loc., *T. Halle 459* (BM, S).

Chile. MAGALLANES: Almirantazgo, 2 Mar. 1908, *T. Halle & C. Skottsberg 456* (PC); Canal Jerónimo, Cutter Cove, 13 Apr. 1908, *T. Halle & C. Skottsberg 458* (PC); s. loc., 25 Apr. 1868, *Cunningham 1261* (MICH); Punta Arenas, Feb. 1906, *R. Thaxter 138* (PC), *167* (PC); Seno Skyring, 25 Apr. 1908, *T. Halle & C. Skottsberg 453* (PC); Seno Otway, 14 Apr. 1908, *C. Skottsberg 454* (PC, S), s. date, *H. N. Mosely* (PC).

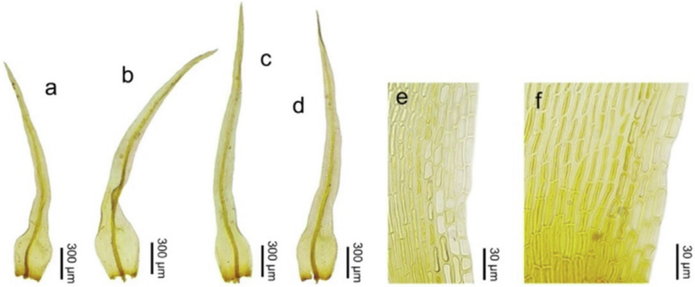


FIG. 103 – *Ulota luteola* (Hook. f. & Wilson) Wijk & Margad. a–d. Leaves. e–f. Marginal cells at leaf base. (All from the isotype of *U. fulvella* in H).

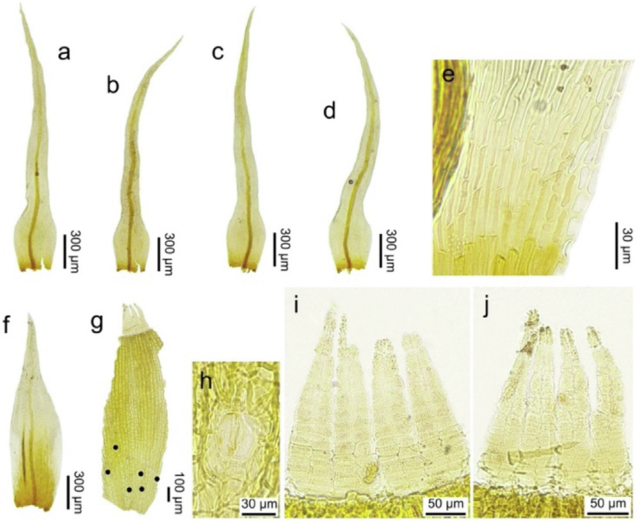


Fig. 104 – *Ulota luteola* (Hook. f. & Wilson) Wijk & Margad. a–d. Leaves. e. Marginal cells at leaf base. f. Perichaetial leaf. g. Exothecial wall, with dots indicating stoma position. h. Stoma. i–j. Peristome. (All from *T. Halle & C. Skottsberg 458* [non-type, S]).

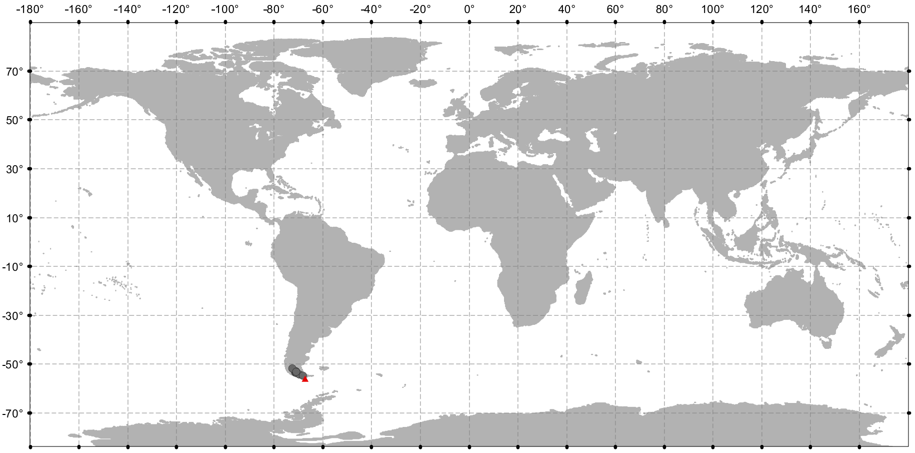


Fig. 105 – Distribution of *Ulota luteola* worldwide. The red triangle indicates the type locality.

26. **Ulota macrocalycina** Mitt., J. Proc. Linn. Soc. 4: 75. 1860. ≡ *Orthotrichum macrocalycinum* (Mitt.) Mitt., J. Linn. Soc., Bot. 12: 190. 1869. Type: Chile. Straits of Magellan, Port Famine, on trunks of trees, Sep. 1851, *Dr. Lyall* (holotype, NY; isotypes, BM000879991–93! PC0099336!).

Ulota marginata (Ångström) A.Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877–78: 427. 1879. ≡ *Orthotrichum marginatum* Ångström, Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 29(4): 4. 1872. Type: Chile. Port Famine, *J. Andressaw* (holotype, S-B172163!). Proposed by Malta (1927) as a synonym of *U. macrocalycina*.

Ulota nothofagi Cardot, Bull.'Herb. Boissier, sér. 2, 5: 1005. 1905. Type: Argentina. " Terre-de-Feu: Ushuaia, troncs de *Nothofagus antartica* et *betuloides*.", 25 Sep. 1902, *C. Skottsberg 85* (lectotype, PC0703855! designated by Wang and Jia, 2016); *C. Skottsberg 84* (paratype, PC0703857! isoparatype, S-B157887! H4334015!); *C. Skottsberg 86* (paratype, PC0703856!). Proposed by Malta (1927) as a synonym of *U. macrocalycina*.

Plants less than 1 cm tall, yellow to green on the top, brown below. Stems are usually creeping, branches abundant. Leaves erect, appressed, and sometimes sinuose when dry, erect-spreading to patent when moist, (1–) 1.1–1.2 (–1.3) mm long; leaf lamina lanceolate, unistratose; leaf base wide, ovate to oblong; apex acute; leaf margin plane, rarely partially recurved; costae strong, ending near the apex. Upper and middle laminal cells irregularly rounded to oblong, (4–) 7–10 (–14) × (5–) 7–9 (–12) μm, thick-walled, with low papillae or smooth; basal inner cells linear, elongate-rectangular and vermicular, (11–) 22–33 (–45) × (2–) 3–5 (–7) μm, smooth, strongly thick-walled; basal marginal cells often differentiated in 4–10 rows, hyaline, quadrate to rectangular, with thin walls.

Autoicous. Perichaetial leaves are much longer, (1.2–) 1.5–1.8 (–2.1) mm long. Vaginula not seen. Seta (1.5–) 1.9–2.4 (–2.5) mm long, slightly twisted anticlockwise when dry. Capsules long exserted, 1.5–1.9 (–2.1) mm long. Urn cylindrical to long cylindrical, strongly constricted when empty and dry, 8-ribbed along the entire length. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, sporadically on the upper part, rarely on the lower part of the urn. Preperistome not seen. Peristome double. Exostome teeth 16, united into 8 pairs, often recurved and lying on the exothecium when dry, lanceolate, densely, and finely papillose on both surfaces. Endostome segments 8, linear, 1/3–1/4 width of teeth at the middle part, yellowish or hyaline, smooth outside, slightly coarse or almost smooth on the inside, almost as tall as teeth. Opercula with a short beak. Calyptrae mitrate, naked. Spores globose, brownish, finely papillose, (24–) 29–33 (–37) μm in diameter.

Illustration: Malta (1927) and Wang and Jia (2016); figures 106 and 107.

Habitat: It grows on trunks of trees, such as *Nothofagus.* There are some records of altitude: (250–) 330–1500 (–1660) m. It is sometimes mixed with *U. magellanica*, *U. billbuckii*, and *Orthotrichum.*

Distribution: It occurs in the southern part of Chile and Argentina. Figure 108.

Notes: *Ulota macrocalycina* is an easily recognized species based on the following combination of characters: erect-appressed leaves, several rows of hyaline cells at basal leaf margins, stomata located on the urn, eight linear endostome segments, and always naked calyptra.

The hyaline cells at basal leaf margins in most *Ulota* species have only transversely thickened walls. But there are thin walls in a few cases, including *Ulota barclayi*, *U. macrocalycina*, *U. pusilla*, and *U. pycnophylla*. These species are all from South America except *Ulota barclayi*, which is from North America. *Ulota barclayi* differs from *U. macrocalycina* in the larger leaves with rounded bases (1.6–1.8 mm), emergent to short exserted capsules, stomata on the transition zone between urn and neck, often sparsely hairy calyptra and smaller spores (19–25 μm). *Ulota pusilla* is distinguished by the larger leaves with rouned bases (1.3–1.5 mm), slightly constricted capsules, 16 endostome segments with strongly coarse and hairy calyptra. *Ulota macrocalycina* is quite similar to *U. pycnophylla*, but the latter differs in often acuminate leaf apex, exostome teeth with papillose-striate inside, stomata on the transition zone between urn and neck, densely hairy calyptra and relatively smaller spores (24–27 μm).

In *Ulota*, *U. barclayi*, *U. hutchinsiae*, *U. macrocalycina*, and *U. pycnophylla* all have the characteristics of often erect-appressed leaves, but *U. hutchinsiae* can be distinguished by the larger leaves (1.5–1.8 mm), hardly differentiated cells at basal leaf margins, stomata occur on the transition zone between urn and neck, much smaller spores (13–14 μm), densely hairy calyptra and saxicolous habit, while the differences of *U. barclayi* and *U. pycnophylla* have been mentioned above.

The stomata in *Ulota macrocalycina* are rarely present at the base of the urn, even at the junction between the urn and neck, such as those in specimens *R. R. Ireland & G. Bellolio 30553 & 36074* (MO).

Key to *Ulota macrocalycina* and its closely related species.

1. Leaf cells at basal margins not or weakly differentiated, with only thickened transverse walls; spores much smaller, 13–14 μm; saxicolous habit .... *U. hutchinsiae*
1. Leaf cells at basal margins distinctly differentiated in 4–10 rows, with thin walls; spores large, 19–35 μm; corticolous habit 2
2. Endostome segments 16, strongly coarse; capsules hardly or slightly constricted when dry .... *U. pusilla*
2. Endostome segments 8, slightly coarse; capsules often strongly constricted when dry 3
3. Leaf base rounded; capsules emergent to short exserted; spores small, 19–25 μm .... *U. barclayi*
3. Leaf base ovate to oblong; capsules long exserted; spores relatively larger, 24–33 μm 4
4. Leaf apex often acuminate; stomata on the transition zone between urn and neck; calyptra densely hairy; exostome teeth with papillose-striate inside; spores small, 24–27 μm .... *U. pycnophylla*
4. Leaf apex acute; stomata often on the urn; calyptra always naked; exostome teeth with densely papillose inside; spores relatively larger, 29–33 μm .... *U. macrocalycina*

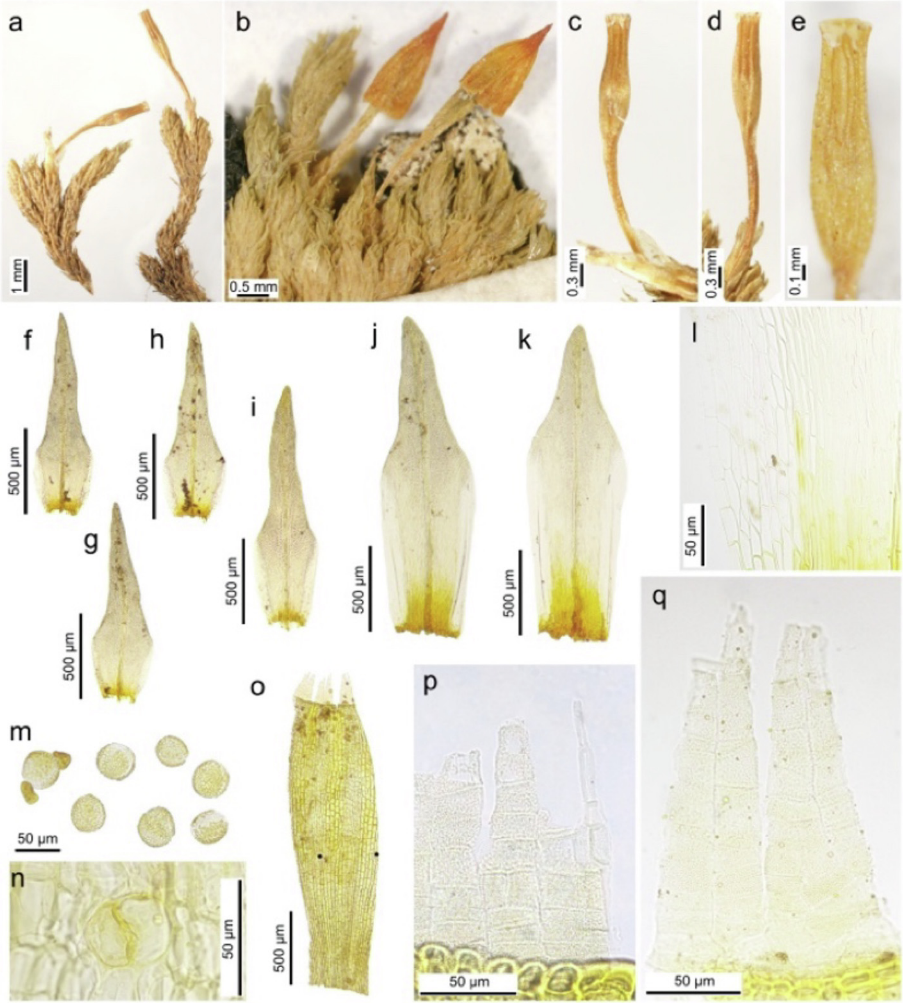


FIG. 106 – *Ulota macrocalycina* Mitt. a–b. Habit with naked calyptra. c–e. Capsules in dry and empty. f–i. Leaves. j–k. Perichaetial leaves. l. Marginal cells at leaf base. m. Spores. n. Stoma. o. Exothecial wall, with dots indicating stoma position. p–q. Peristome. (All from the isotypes in BM except p from *R. R. Ireland & G. Bellolio 30553* [non-type, MO]).

Additional Specimens Examined: **Argentina**. CHUBUT: Lago Menéndez, 21 Jan. 1938, *A. Kalela B248j(2)* (H). NEUQUÉN: Lago Aluminé, 24 Dec. 1937, *A. Kalela B154e-3* (H), *B154f* (H), 28 Dec. 1937, *B179b* (H); Lago Quillén, *A. Kalela B179b* (H). RÍO NEGRO: Parque National de Nahuel Huapi, Lago Massardi, Oct. 1936, *A. Donat s.n.* (S). TIERRA DEL FUEGO: Ushuaia, s. date, *s.coll.* (S), 1902, *C. Skottsberg 84* (H), 1 May 1896, *P. Dusén s.n.-1* (H), 5 May 1896, *366(2)* (S-B158007).

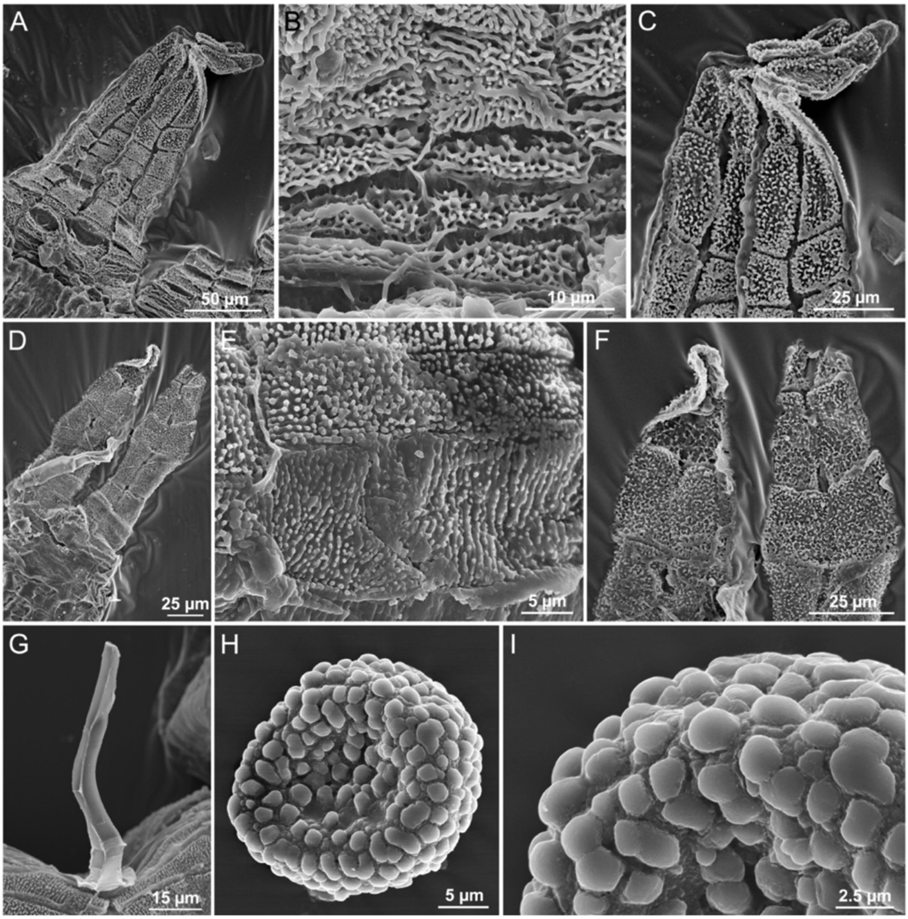


FIG. 107 – *Ulota macrocalycina* Mitt. A, outer surface of exostome; B, outer surface of basal exostome; C, outer surface of upper exostome; D, inner surface of exostome; E, inner surface of basal exostome; F, inner surface of upper exostome; G, outer surface of endostome; H, a spore; I, surface ornamentation of a spore. (All from *C. J Cox no.319/00* [non-type, DUKE] except A, C, D & F from the isotype in BM).

Chile. ARAUCANÍA: Malleco Prov., 27 Oct. 1998, *B. Goffinet 5487a* (DUKE). BÍO-BÍO: Nuble, 5–7 Dec. 2002, *R. R. Ireland & G. Bellolio 30553* (MO), *30658* (MO), 17 Nov. 2002, *34420* (MO). MAGALLANES: Brunswick Peninsula, 14 Mar. 2000, *C. J. Cox & B. Goffinet 21/00* (DUKE), 13 Mar. 2000, *14/00* (DUKE); Estancia Vicuna, 31 Dec. 1928, *H. Roivainen s.n.* (H); Lago del Toro, 10 Mar. 1941, *R. Santesson M788* (S); Laguno El Parrillar, 21 Dec. 1967, *J. J. Engel 2074a* (H); Punta Arenas, 21 Nov. 1895, *P. Dusén 15(2)* (S), 29 Nov. 1895, *88* (S), 12 Feb. 1938, *A. Kalela B304d* (H); Rio Rubens, near Hotel Rio Rubens, 12 Jan. 1941, *R. Santesson M456* (S); Tierra del Fuego, Canal Beagle, Feb. 1920, *s.coll.* (S),

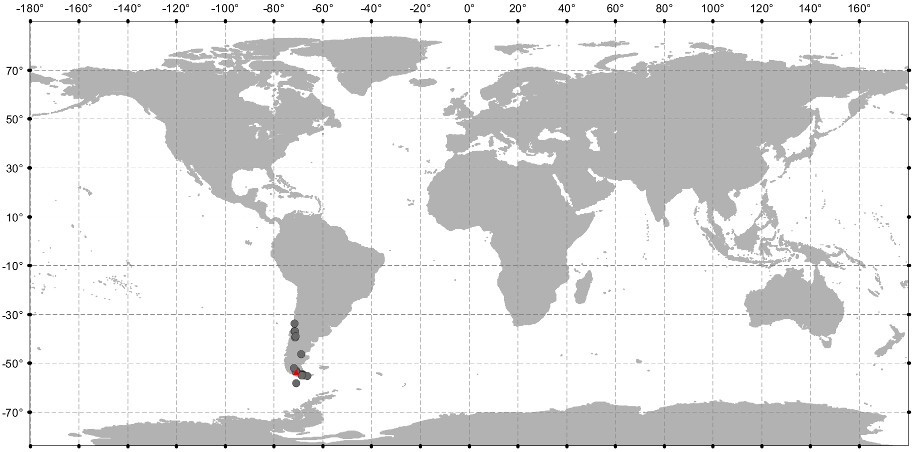


Fig. 108 – Distribution of *Ulota macrocalycina* worldwide. The red triangle indicates the type locality.

M. Gusinde s.n. (H4334027–28), Island Navarino, 18 Mar. 2000, *C. J. Cox 319/00* (DUKE), 17 Mar. 2000, *198/00* (DUKE).

27. **Ulota macrodontia** Dixon & Malta, Acta Horti Bot. Univ. Latv. 2: 202. 1927. Type: Chile. Río Aysén, 1897, *P. Dusén s.n.* (lectotype, S-B157812! designated by Garilleti *et al.*, 2016); in ramulis, 14 Jan. 1897, *P. Dusén 434* (paratype, H4334014!).

Plants 0.5–1 cm tall, green to olive-green above, brown below. Stems usually branched. Leaves moderately crisped when dry, patent to wide-spreading when moist, (1.1–) 1.3–2.1 (–2.5) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded to oblong, (5–) 7–12 (–15) × (6–) 8–9 (–11) μm, thick-walled, with low papillae; basal inner cells linear, elongate-rectangular, (16–) 25–33 (–38) × (2–) 3–4 (–5) μm, with slightly to the moderately thickened wall, smooth; basal marginal cells often differentiated in 4–6 rows, hyaline, quadrate to rectangular, with thin or equally slightly thickened walls.

Autoicous. Perichaetial leaves are distinctly longer, 1.6–1.9 mm. Vaginula not seen. Seta 3–5 mm long, sometimes twisted anticlockwise when dry. Capsule long exserted, ca. 0.8 mm long. Urn cylindrical, slightly constricted below the mouth when dry and empty, with eight inconspicuous ribs. Neck short, abruptly narrowed to the seta. Exothecial cells indistinctly differentiated into eight bands, almost as long as an urn, often three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial sporadically occurs on the urn. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, incurved when dry, lanceolate, strongly, and densely papillose on both sides. Endostome segments 8, linear, almost as tall as teeth, uniseriate, dark yellow, ca. 1/3 width of teeth, smooth on the outside, strongly and densely papillose on the inside. Opercula not seen. Calyptra mitrate, densely hairy. Spores spherical, more coarsely papillose, (29–) 33–41 (–47) μm in diameter.

Illustration: Malta (1927) and Garilleti *et al.* (2016, 2021); figure 109.

Habitat: No phorophyte and altitude records were found in this study. But it is reported (Garilleti *et al.*, 2021) that this species always grows on branches and twigs of trees and shrubs, including *Aextoxicon*, *Azara*, *Berberis*, *Castanea*, *Eucryphia*, *Fuchsia*, *Malus*, *Nothofagus*, *Raukaua*, *Rhaphithamnus*, *Ribes*, *Salix*, *Sambucus*, and *Weinmannia*, and its altitude ranges from sea level to 1700 m.

Distribution: It occurs in Chile, rarely in Argentina, as reported by Garilleti *et al.* (2021). Figure 110.

Notes: *Ulota macrodontia* is a species rarely studied for a long time until recently, some controversy about its circumscription caused by the very mixed type materials (Garilleti *et al.*, 2016; Wang and Jia, 2016). The essential problem between them is which type collection is more identical to the protologue of *Ulota macrodontia* (Malta, 1927). Wang and Jia (2016) selected S-B157813, while T. Seki (1972 in herbarium) and Garilleti *et al.* (2016) chose S-B157812. Garilleti *et al.* (2016) considered that their lectotype is closer to the original description and soon superseded the one designated by Wang and Jia (2016). However, they did not make a detailed morphological comparison between the related type materials and the original publication but only provided two photos of the appearance of S-B157812 and some sporophytic characters of a non-type specimen. Therefore, we have summarized all the key characters mentioned before in the related type specimens and the protologue (table 1). Unfortunately, it is impossible for us to make a decision based on the current results because some characters need to be determined by re-examining the type specimens, which is not available to us now. Considering this, we temporarily accept the treatment of Garilleti *et al.* (2016) here.

According to Garilleti *et al.* (2016, 2021), *Ulota macrodontia* is characteristic of incurved exostome teeth when dry, eight linear endostome segments with strongly papillose, systylous lids and small spores (15–24 μm). The incurved exostome teeth occasionally can be seen in other species of *Ulota* in our study, but we have never seen any species whose exostome teeth are always, or at least mostly, incurved when dry and mature. This is very unusual in the genus *Ulota*. Detailed comments can also be found in the Peristome of Morphology. The character of systylous lids is a similar case. The spore size also varies greatly in different studies, even the two results both from Garilleti *et al.* (figure 1D in 2016 *vs.* figure 2I in 2021). We cannot judge all these mentioned above until we see more materials. Nevertheless, *Ulota macrodontia* is still a “good species”, which can be easily distinguished by its strongly papillose endostome segments, combined with several rows of thin-walled hyaline cells at leaf basal margins.

Ulota macrodontia resembles *Ulota pusilla* locally very much. Both have hardly constricted capsules, urn-located stomata, distinctly ornamentated narrow endostome segments, and hairy calyptra. But *Ulota pusilla* can be distinguished by the

Tab. 1 – Comparison of main characters between Malta's protologue (1927) and type materials. The gray color shows the consistent characters between them.

	Malta's protologue		Type materials		
	Description	Illustration	S-B157812	S-B157813	H4334009 partial (only one individual with single capsule)
			H4334014	H4334009 partial	
Hyaline cells at basal leaf margins	many rows, often to the middle of the lamina, thin-walled	not shown	several rows, thickness of transverse walls unknown	ca. 10 rows, with only thickened transverse walls	unknown
Capsule	long-cylindrical, constricted at the mouth, up to 2 mm long	cylindrical to long-cylindrical, constricted at the mouth, with operculum	cylindrical, not constricted, without operculum	cylindrical, more or less constricted at the mouth, with operculum	long-cylindrical, slightly constricted at the mouth, with operculum
Exostome teeth	incurved when dry	incurved when dry	incurved when dry	recurved when dry	incurved when dry
Endostome segments	8, with needle-like papillose	8, strongly papillose	8, needle-like papillose	16, smooth	unknown
Calyptra	not shown	campanulate	conic	campanulate	unknown
Spore size	16–21 μm	not shown	33–41 μm	37–41 μm	unknown

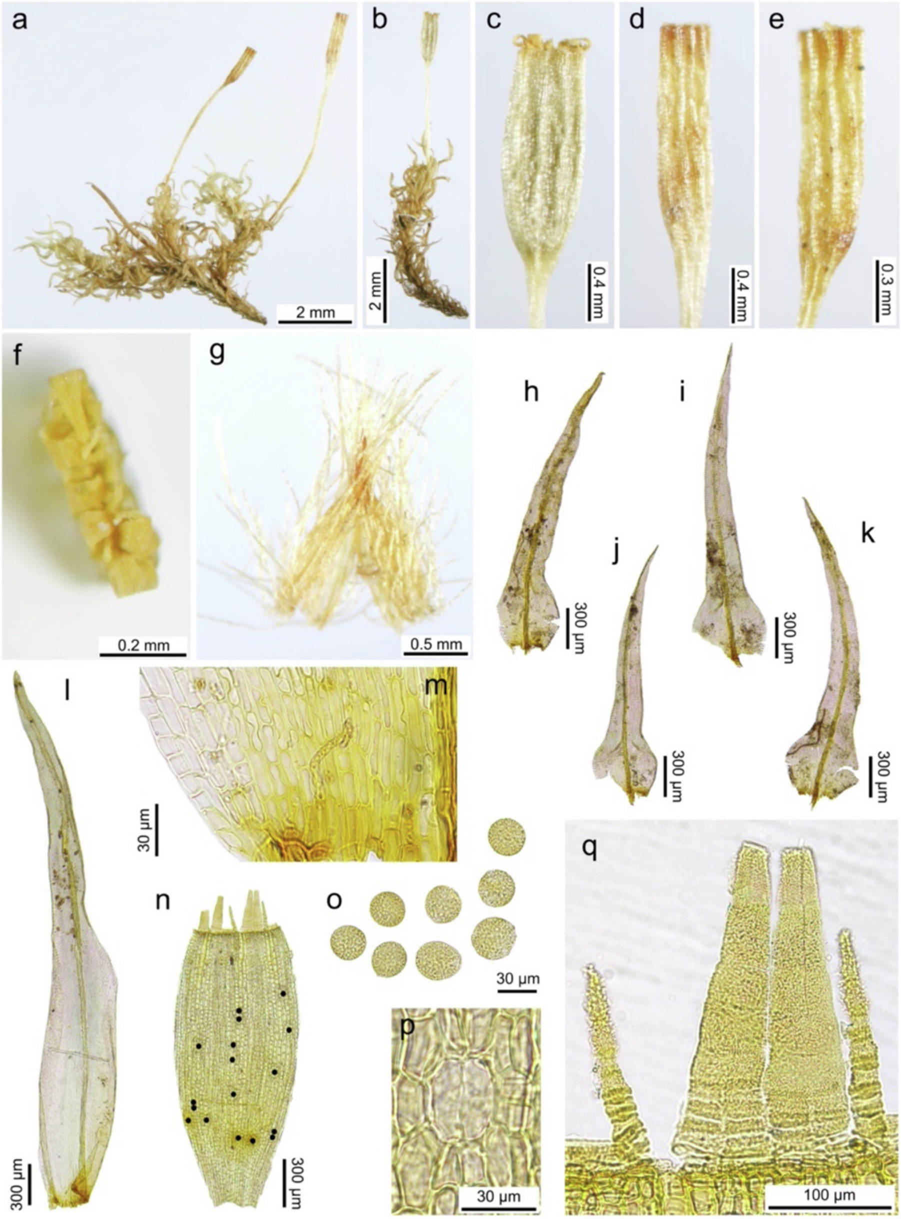


FIG. 109 – *Ulota macrodontia* Dixon & Malta. a–b. Habit. c–e. Capsules in dry and empty. f. Capsule mouth viewed from above. g. Calyptra. h–k. Leaves. l. Perichaetial leaf. m. Leaf basal cells. n. Exothecial wall, with dots indicating stoma position. o. Spores. p. Stoma. q. Peristome. (a–g from the lectotype in S [B157812], h–q from *M. Gusinde s.n.* [non-type, S]).

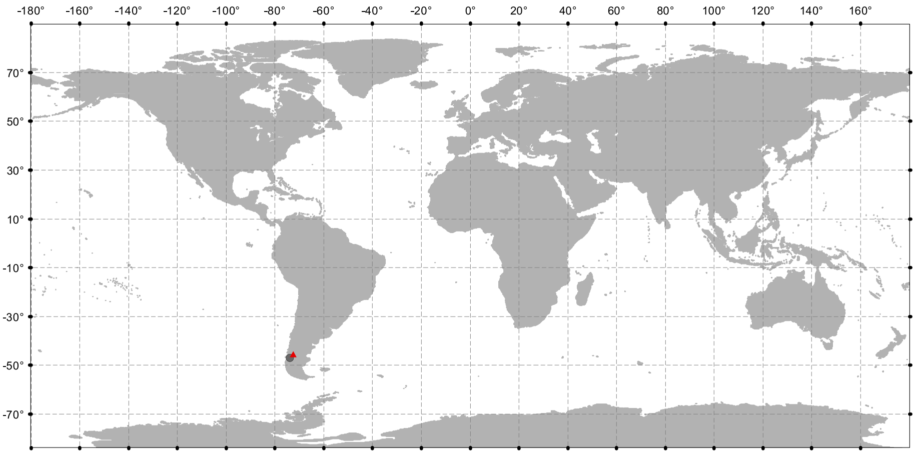


FIG. 110 – Distribution of *Ulota macrodontia* worldwide. The red triangle indicates the type locality.

often 16 endostome segments with relatively weaker ornamentation and flexuose leaves with much wider bases.

Key to *Ulota macrodontia* and its closely related species.

1. Endostome segments 16, distinctly finely papillose or striate but weaker than exostome teeth; leaves flexuose or rarely crisped when dry; leaf bases much wider, with 5–10 rows of hyaline cells at margins................................ *U. pusilla*
1. Endostome segments 8, strongly and densely papillose as much as exostome teeth; leaves moderately crisped when dry; leaf bases relatively narrower, with 4–6 rows of hyaline cells at margins... *U. macrodontia*

Additional Specimens Examined: **Chile**. AYSÉN: San Rafael, Feb. 1921, *M. Gusinde s.n.* (S).

28. **ULOTA MAGELLANICA** (Mont.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 164. 1874. ≡ *Orthotrichum magellanicum* Mont., Ann. Sci. Nat., Bot., sér. 2, 19: 242. 1843. TYPE: CHILE. Magellan, Port Famine, *M. Jaequinot* (lectotype, PC0094404! designated by Wang and Jia, 2016).

Ulota hamata Dusén, Rep. Princeton Univ. Exp. Patagonia, Botany 8(3): 82. 1903. TYPE: CHILE. "Patagonia australis in truncis arborum", 1897, *J. B. Hatcher 67* (holotype, S-B157810! isotypes, PC! NY). Proposed by Wijk *et al.* (1969) as a synonym of *U. magellanica.*

Plants less than 1 cm tall, green above, brown to black below. Stems usually branched. Leaves erect, sinuose and falcate when dry, patent when moist, (1.2–) 1.5–2 (–2.6) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded, concave; apex acuminate; leaf margin plane, rarely partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded or oblong, (6–) 8–11 (–14) × (6–) 10–13 (–14) μm, thick-walled, with low papillae; basal inner cells linear, rhomboidal, elongate-rectangular, (14–) 19–25 (–31) × 2–3 (–5) μm, with strongly thickened wall, smooth; basal marginal cells weakly differentiated, no more than three rows, hyaline, quadrate to rectangular, with transversely thickened walls.

Autoicous. Perichaetial leaves somewhat longer, (2–) 2.1–2.4 (–2.6) mm. Vaginula is strongly hairy. Seta (2–) 2.5–3.4 (–4) mm long, twisted anticlockwise when dry. Capsule long exserted, 1–1.4 mm long. Urn cylindrical and strongly constricted below the mouth when dry and empty, with eight furrows along the entire length, with prominent ribs alternately. Neck slightly long, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, scattered on the lower half of the urn or at the base of the urn. Preperistome rarely seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, lying on the exothecium, lanceolate, densely papillose on the outside, finely striate, or rarely papillose on the inside. Endostome segments 16, lanceolate, free at the base, almost as tall as teeth, eight segments often irregularly biseriate, as wide as teeth, eight alternately uniseriate, little narrower than teeth, hyaline, smooth on the outside, slightly scabrous on the inside. Opercula with a short beak. Calyptra mitrate, sparsely hairy to nearly naked, sometimes moderately to densely hairy. Spores spherical, finely papillose, large, unicellular, (27–) 36–44 (–52) μm in diameter.

Illustration: Malta (1927) and Wang and Jia (2016); figures 111 and 112.

Habitat: It grows on trunks of trees, such as *Nothofagus*. There are a few records of altitude: (10–) 380–1630 (–1660) m. It is usually mixed with *Ulota macrocalycina*, sometimes with *U. luteola* and *Orthotrichum*.

Distribution: It only occurs in the southern part of Chile and Argentina. Figure 113.

Notes: *Ulota magellanica* is a quite remarkable species, characterized by non-crisped leaves, little differentiated basal marginal leaf cells, 16 broad endostome segments, and large spores. Recently, two new species were described by Garilleti *et al.* (2012, 2015) from the same area, *i.e. Ulota billbuckii* and *U. larrainii.*

They are closely related to *Ulota magellanica* in some important characteristics, including the situation of leaves when dry, differentiation of basal marginal leaf cells, the configuration of endostome segments, and spore size. However, the striking difference between *Ulota billbuckii* and *U. larrainii* from *U. magellanica* is the multicellular spores and endostome segments connected at the lower part of *U. billbuckii.*

The hairiness of calyptra in *Ulota magellanica* varies greatly, from nearly naked, sparsely hairy to densely hairy. In the specimens observed by us, sparsely hairy is a little more common.

Key to *Ulota magellanica* and its closely related species.

1. Spores unicellular, 36–44 μm.. *U. magellanica*
1. Spores multicellular, 85–140 μm...2
2. Endostome segments remarkably connected by some cells at lower half part.. *U. billbuckii*
2. Endostome segments almost free at the base.................................... *U. larrainii*

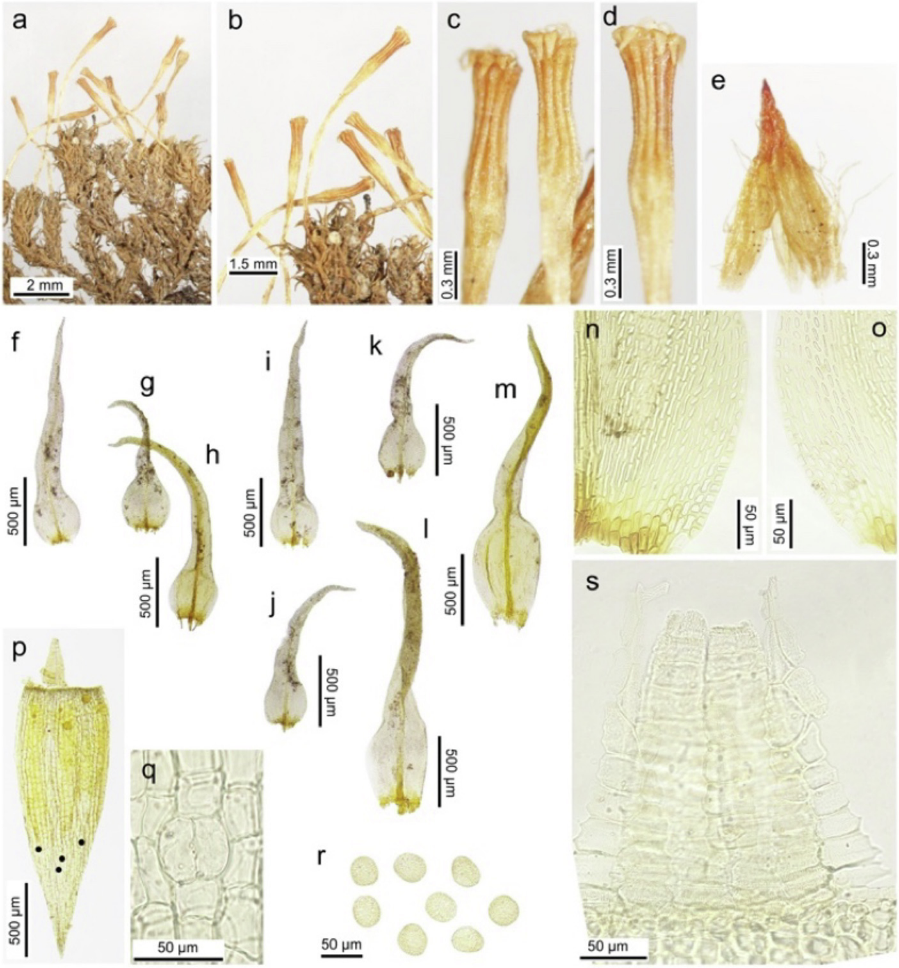


FIG. 111 – *Ulota magellanica* (Mont.) A. Jaeger. a–b. Habit. c–d. Capsules in dry and empty. e. Calyptra. f–k. Leaves. l–m. Perichaetial leaves. n–o. Marginal cells at leaf base. p. Exothecial wall, with dots indicating stoma position. q. Stoma. r. Spores. s. Peristome. (All from the lectotype in PC except n and o, r–s from *R. R. Ireland & G. Bellolio 36077* [non-type, MO]).

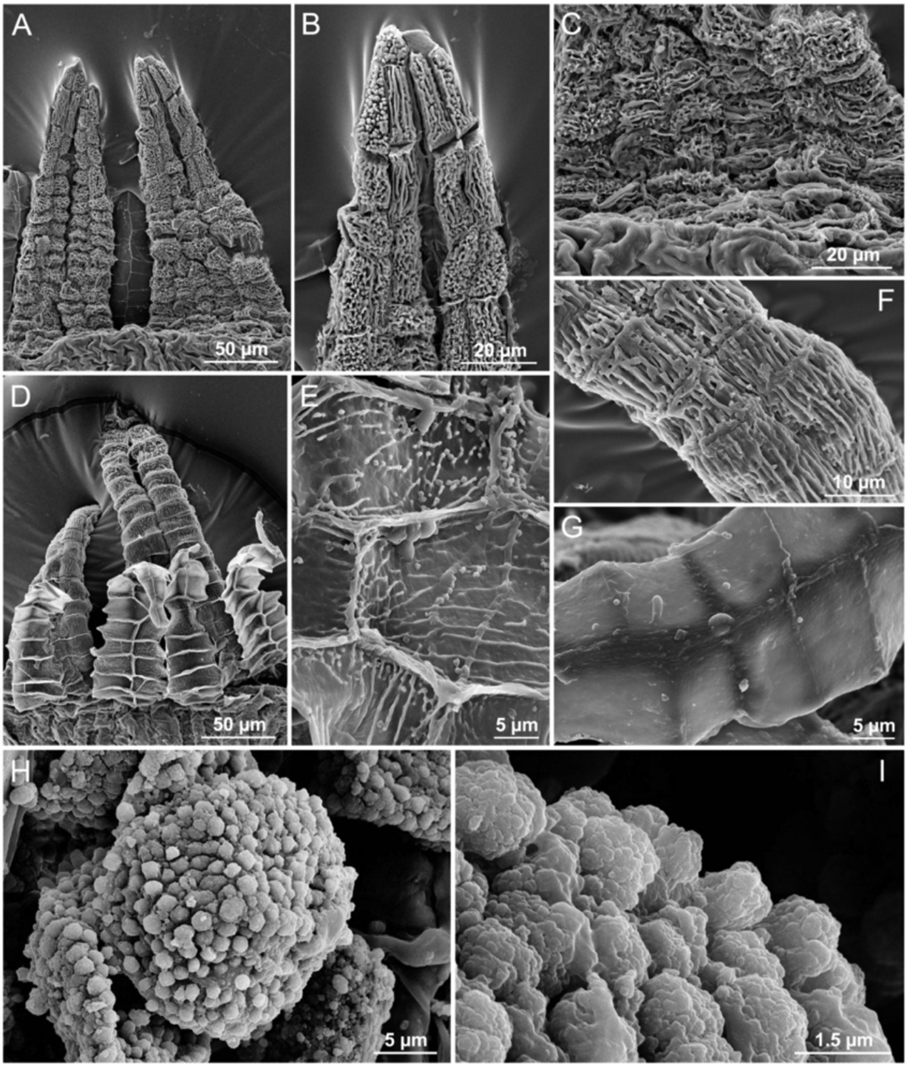


FIG. 112 – *Ulota magellanica* (Mont.) A. Jaeger. A, outer surface of exostome; B, outer surface of upper exostome; C, outer surface of basal exostome; D, inside view of exostome and endostome; E, inner surface of endostome; F, inner surface of middle exostome; G, outer surface of endostome; H, spores; I, surface ornamentation of a spore. (All from *N. J. Andersson* [non-type, S] except E–G from the lectotype in PC).

Additional Specimens Examined: **Argentina**. CHUBUT: Lago Futalaufquén, 18 Jan. 1938, *A. Kalela B234b* (H). NEUQUÉN: Lago Correntoso, 17 Nov. 1937, *A. Kalela B47f* (H). TIERRA DEL FUEGO: Estancia Basmen, 16 Jan. 1929, *H. Roivainen s.n.-2* (H); Ushuaia, 5 May 1896, *P. Dusén 366* (S-B157962, S-B158011), *366(1)* (S-B158007), 25 Sep. 1902, *C. Skottsberg 88* (S, PC), 30 Sep. 1902, *89* (S-B157958–59, PC).

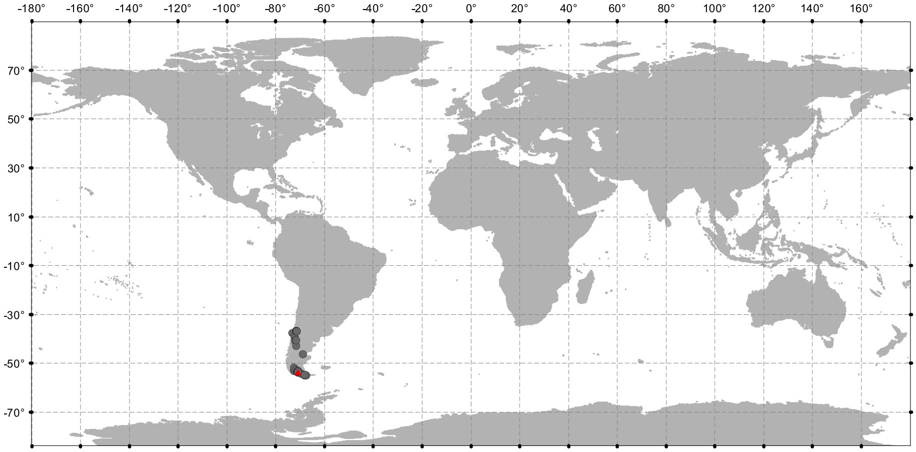


FIG. 113 – Distribution of *Ulota magellanica* worldwide. The red triangle indicates the type locality.

Chile. ARAUCANÍA: Villarrica, Feb. 1977, *I. Barends 10715* (MO). BÍO-BÍO: Arauco, 30 Oct. 2001, *R. R. Ireland & G. Bellolio 33040* (BM, MO); Ñuble, 5–7 Dec. 2002, *R. R. Ireland & G. Bellolio 30673* (MO), 17 Nov. 2002, *34420* (BM), 18 Nov. 2002, *34501* (MO), 12 Feb. 2003, *36077* (MO). LOS LAGOS: Osorno, 23 Mar. 2000, *C. J. Cox 595/00* (DUKE). MAGALLANES: Brunswick Peninsula, 3 Nov. 1998, *B. Goffinet 5648* (DUKE), 13 Mar. 2000, *C. J. Cox & B. Goffinet 14/00* (DUKE); Island Riesco, 30 Apr. 1940, *R. Santesson M554* (S); Punta Arenas, 21 Nov. 1895, *P. Dusén 15(1)* (S), Jun. 1905, *R. Thaxter 166* (MICH), 8 Feb. 1938, *A. Kalela B287c* (H), 11 Feb. 1938, *A. Kalela B296a* (H), Laguno El Parrillar, 21 Dec. 1967, *J. J. Engel 2074b* (H); Port Famine, s. date, *N. J. Andersson s.n.* (S), Sep. 1851, *D. Lyall* (BM000876995, BM000919506), *D. Lyall (2)* (BM000919504), *D. Lyall (1)* (BM000876996, BM000919505), s. date, *Jacquinot s.n.* (BM); Rio Rubens, 5 Feb. 1938, *A. Kalela B271c* (H); Tierra del Fuego, Almirantazgo, 9 Mar. 1908, *T. Halle et C. Skottsberg 460-1* (PC), Island Navarino, 17 Mar. 2000, *C. J. Cox 198/00* (DUKE), 18 Mar. 2000, *351a/00* (DUKE).

29. **ULOTA MALTIANA** Garilleti & F. Lara, Bryologist 123(2): 165. 2020. TYPE: CHILE. Región Aysén del General Carlos Ibáñez del Campo: Provincia de Aysén, Comuna de Cisens, Parque Nacional Queulat, entrance to Ventisquero Colgante, 44°28′17″ S, 72°33′34″ W, 40 m, moss forest of *Nothofagus betuloides*, on *N. dombeyi*, 28 Dec. 2016, *R. Garilleti 2016-231a & F. Lara* (holotype, VAL-Briof 11822; isotypes, CONC, BM, MAUAM).

Ulota germana var. *breviseta* Malta, Acta Horti Bot. Univ. Latv. 2: 202. 1927. TYPE: CHILE. Río Aysén, Jan. 1897, *P. Dusén 434* (lectotype, H4334009! (partial), designated by Garilleti *et al.*, 2020; isolectotype, S-B157813! (partial)).

Plants 0.5–1 cm tall, yellow to brown above, dark brown to black below. Stems usually branched. Leaves strongly crisped when dry, patent to wide-spreading when moist, (2–) 2.2–2.9 (–3) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex acuminate; leaf margin plane, sometimes partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded to oblong, (8–) 10–12 (–13) × 7–8 (–9) μm, thick-walled, with ca. 2 low papillae per cell; basal inner cells linear, elongate-rectangular, vermicular, (24–) 32–38 (–47) × (5–) 6 (–7) μm, with thick wall, smooth; basal marginal cells often differentiated in ca. 10 rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves distinctly longer, (2.9–) 3–3.7 (–3.8) mm. Vaginula naked. Seta 2–3.6 mm long, sometimes twisted anticlockwise when dry. Capsule long exserted, ca. 1.4 mm long. Urn cylindrical, moderately constricted below the mouth when dry and empty, with eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, often four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial occurs on the central or lower part of the urn. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry and lying on the exothecium, lanceolate, densely papillose on the outside, striate on the inside. Endostome segments 16, linear-lanceolate, almost as tall as teeth, uniseriate or biseriate, hyaline, 1/2–1/3 width of teeth, smooth on the outside, nearly smooth or slightly coarse on the inside. Opercula not seen. Calyptra mitrate, densely hairy. Spores spherical, more coarsely papillose, (34–) 37–41 (–43) μm in diameter.

Illustration: Garilleti *et al.* (2020); figures 114 and 115.

Habitat: No phorophyte and altitude records were found in this study. But it was reported by Garilleti *et al.* (2020) as growing at 0–150 (–730) m in altitude and on trunks or branches of trees or shrubs, including *Aextoxicon*, *Azara*, *Berberis*, *Caldcluvia*, *Castanea*, *Eucryphia*, *Fuchsia*, *Gaultheria*, *Malus*, *Nothofagus*, *Pinus*, *Ribes*, *Salix*, and *Weinmannia*.

Distribution: It is **endemic** to Chile. Figure 116.

Notes: Although the name *Ulota maltiana* has just been published most recently, it actually has been found earlier as *U. macrodontia* (Wang and Jia, 2016). This is a dispute on the circumscription of *Ulota macrodontia*; please refer to it for details.

The most prominent characteristics of *Ulota maltiana* are the strongly crisped leaves, many rows of hyaline cells at basal leaf margins, 16 narrow endostome segments, stomata scattered on the urn, and densely hairy calyptra.

Ulota maltiana is closely related to *Ulota crispa* in the crisped leaves, remarkably differentiated basal leaf margin, narrow endostome segments, and densely hairy calyptra. However, *Ulota crispa* is different in the stomata confined to the transitional zone between the urn and neck, usually eight endostome segments and smaller spores (19–25 μm). *Ulota maltiana* also resembles Chinese *U. morrisonensis* in the strongly crisped leaves, 16 narrow endostome segments, and densely hairy calyptra. But *Ulota morrisonensis* is distinguished by the less rows (3–6) of hyaline cells at basal leaf margins, stomata restricted to the transitional zone between urn and neck,

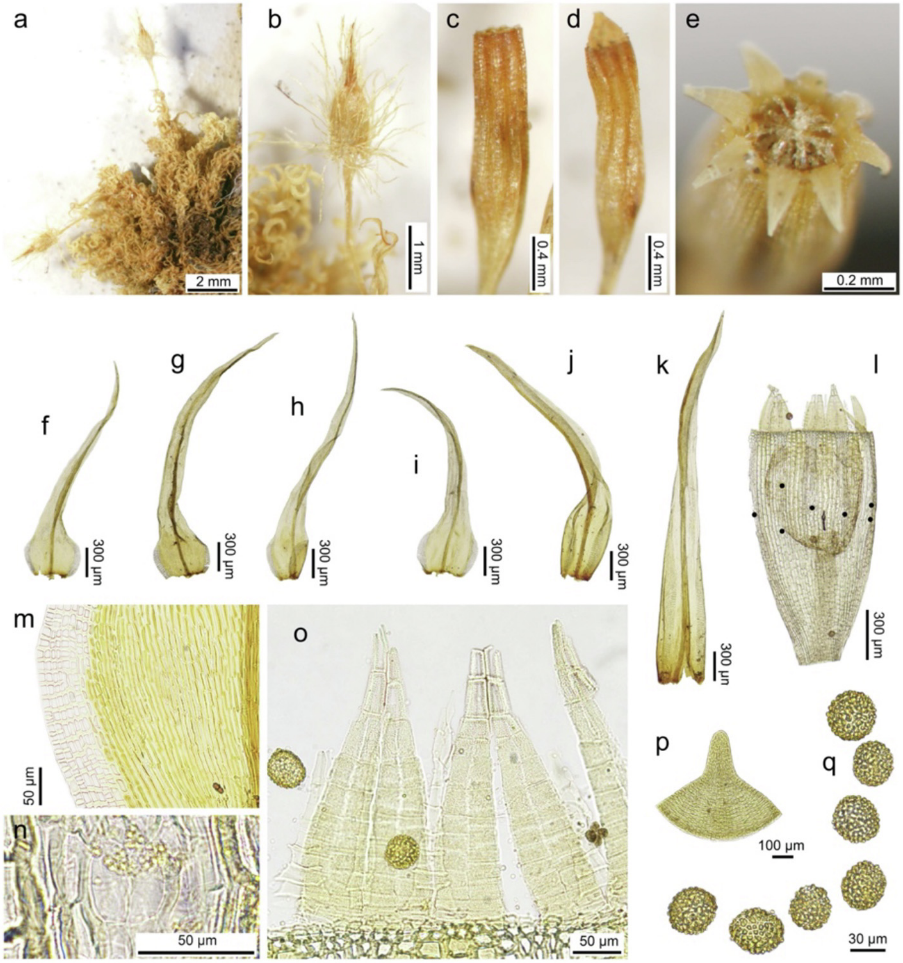


Fig. 114 – *Ulota maltiana* Garilleti & F. Lara. a. Habit. b. Calyptra. c–d. Capsules in dry. e. Capsule mouth viewed from above. f–i. Leaves. j–k. Perichaetial leaves. l. Exothecial wall, with dots indicating stoma position. m. Marginal cells at leaf base. n. Stoma. o. Peristome. p. Operculum. q. Spores. (All from *P. Dusén 434* [non-type, S-B157813]).

larger leaves (2.5–4.1 mm), longer seta (5.3–7 mm), and neck and smaller spores (24–27 μm).

Key to *Ulota maltiana* and its closely related species.

1. Stomata on the central or lower part of urn; seta shorter, 2–3.6 mm; spores large, 37–41 μm...*U. maltiana*

1. Stomata on the junction between urn and neck; seta longer, 3–7 mm; spores small, 19–27 μm...2

2. Hyaline cells at basal leaf margins with more rows (5–11); endostome segments often 8; leaves smaller, 2.1–2.6 mm; seta shorter, 3–5 mm.................. *U. crispa*
2. Hyaline cells at basal leaf margins with less rows (3–6); endostome segments 16; leaves larger, 2.5–4.1 mm; seta longer, 5.3–7 mm.................... *U. morrisonensis*

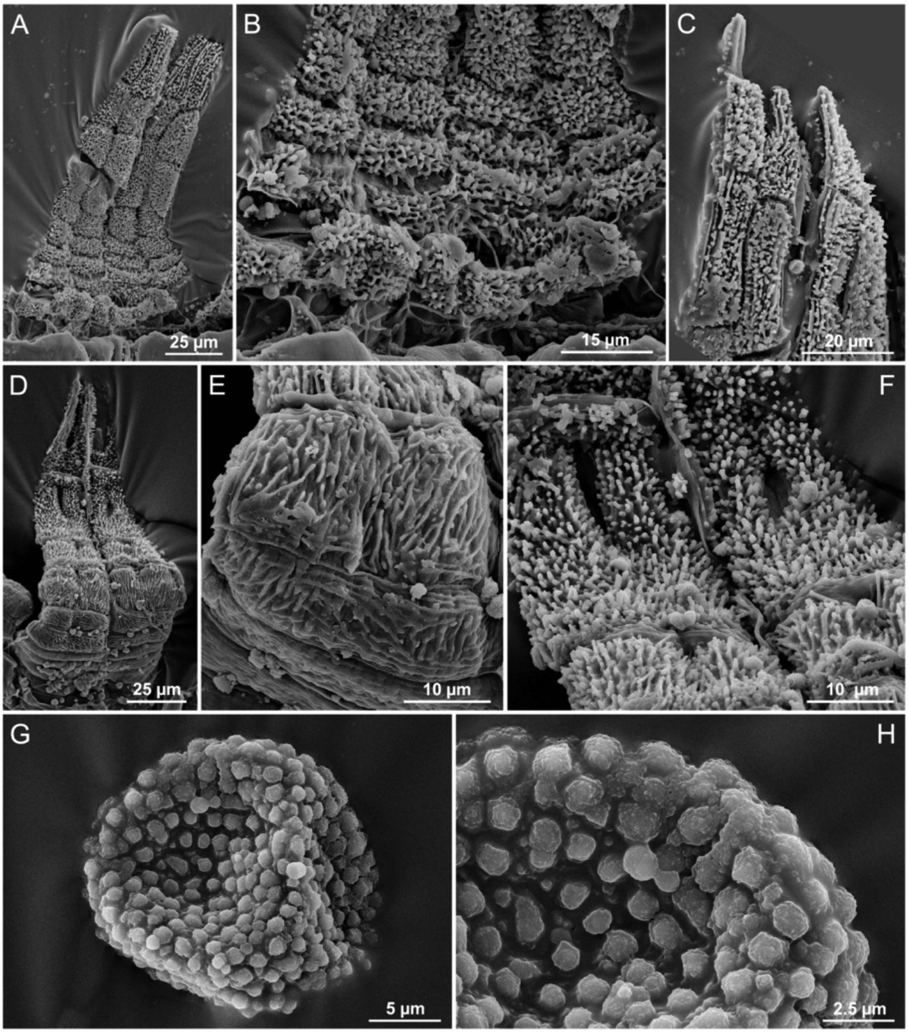


FIG. 115 – *Ulota maltiana* Garilleti & F. Lara. A, outer surface of exostome; B, outer surface of basal exostome; C, outer surface of upper exostome; D, inner surface of exostome; E, inner surface of basal exostome; F, inner surface of upper exostome; G, a spore; H, surface ornamentation of a spore. (All from *P. Dusén 434* [non-type, H4334009]).

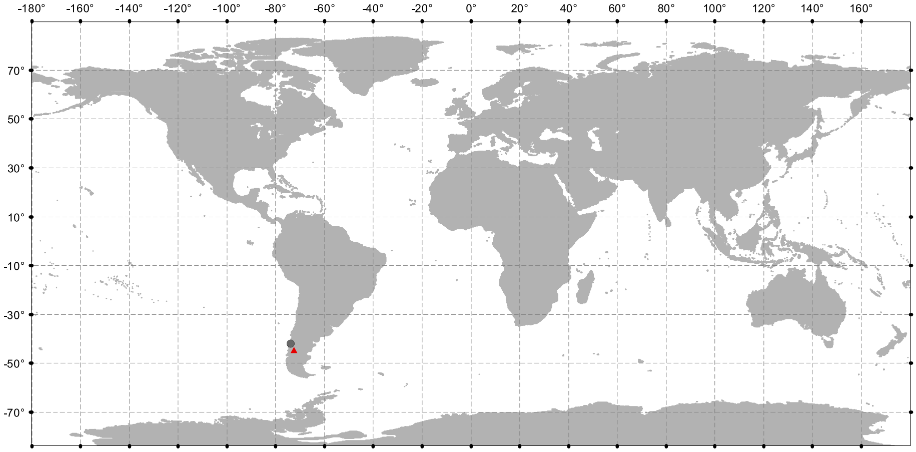


FIG. 116 – Distribution of *Ulota maltiana* worldwide. The red triangle indicates the type locality.

Additional Specimens Examined: **Chile**. AYSÉN: San Rafael, Feb. 1921, *M. Gusinde s.n.* (S). LOS LAGOS: Chiloe Island, Aucud, 11 Mar. 1932, *Carl O. Enla..son 126(1)* (MICH), 23–25 Jan. 1948, *B. Sparre 4150* (S).

30. **ULOTA MEGALOSPORA** Venturi, Bot. Centralbl. 44: 389. 1890. TYPE: U.S.A. Washington, Cascaden, Rigi prope Clealum Lake, *Röll*, 1889 (lectotypes, FH00059353! designated by Vitt, 1970; isolectotype, NY00524132!).

Ulota subulata Kindb., Catalogue of Canadian Plants, Part VI, Musci 82. 1892. ≡ *Orthotrichum subulatum* (Kindb.) Kindb., European and N. American Bryineae (Mosses) 2: 305. 1897. *illegitimate, later homonym.* TYPE: CANADA. British Columbia, near New Westminster Junction, along the Coquhilla River, Black's Farm, on small trees in thickets, 26 Apr. 1889, *J. Macoun* (holotype, S-B181365!).

Ulota subulifolia Müll. Hal. & Kindb., Catalogue of Canadian Plants, Part VI, Musci 82. 1892.

Plants less than 1 cm tall, yellow to green above, brown to black below. Stems usually branched. Leaves flexuose and weakly crisped when dry, patent when moist, (0.7–) 1.2–1.7 (–2.3) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded or oblong, (6–) 9–13 (–16) × (4–) 6–9 (–11) μm, thick-walled, with low papillae; basal inner cells linear, sigmoid, rectangular to elongate-rectangular, (12–) 18–30 (–41) × (1–) 2–4 (–6) μm, with strongly thickened wall, smooth; basal marginal cells weakly differentiated, only one, rarely up to three rows, hyaline, quadrate to rectangular, with transverse walls more thickened.

Autoicous. Perichaetial leaves somewhat longer, (2.1–) 2.2–2.3 (–2.5) mm. Vaginula sparsely hairy, uniseriate, smooth, hyaline. Seta (1.8–) 3–4.5 (–5.3) mm long, slightly twisted anticlockwise when dry. Capsule long exserted, 1–1.4 (–1.5) mm long. Urn short-cylindrical to cylindrical, slightly, sometimes moderately constricted below the mouth when dry and empty, eight furrows along the entire length, with prominent ribs alternately. Neck long when the urn is dry and empty, gradually narrowed to the seta. Exothecial cells differentiated into eight bands, almost as long as an urn, usually four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the base of the urn or the junction between the urn and neck, or the central part of capsules. Preperistome rarely seen. Peristome double. Exostome teeth 16, united into 8 pairs, recurved when dry, sometimes lying on the exothecium, lanceolate, densely papillose below and striate above on the outside, striate or striate-papillose on the inside. Endostome segments 8, linear to narrow-lanceolate, almost reaching the exostome teeth, uniseriate, often biseriate at the lower part, 1/3–1/4 width of teeth, hyaline, smooth on the outside, slightly scabrous on the inside. Opercula with a short to medium-long beak. Calyptra mitrate, sparsely, rarely densely hairy. Spores spherical, finely papillose, (27–) 41–51 (–65) μm in diameter.

Illustration: Vitt (2014); figures 117 and 118.

Habitat: It grows on trunks or branches of trees, such as *Abies*, *Acer*, *Alnus* (alder), birch, *Pinus*, *Pseudotsuga*, *Rubus*, *Salix* (willow), and *Tsuga*. There are some records of altitude: (335–) 564–1206 (–1600) m. It is sometimes mixed with *Ulota barclayi* and *Orthotrichum sp.*

Distribution: It is only found on the west coast of North America. The recent report from Japan is discussed below. Figure 119.

Notes: *Ulota megalospora* is characterized by large spores, just like its name. Besides that, its non-crisped leaves, hardly differentiated basal leaf marginal cells, long neck, and often sparsely hairy calyptra are important diagnostic characteristics. It is worth noting that due to its long neck of dry capsules, the stomatal in *Ulota megalospora* can be described as a central part of capsules or at the urn-base or the junction between the urn and neck.

Recently, *Ulota megalospora* has been reported from Japan (Suzuki and Iwatsuki, 2013), which is the first record outside North America. However, according to their description and illustration, this Japanese material is obviously not consistent with those from North America observed by us, including crisped and larger leaves (1.9–2.3 mm), longer capsules (2.5–2.8 mm), short seta (1.8–2.4 mm) and relatively small spores (28–50 μm), but somewhat similar to *Ulota reptans.* Likewise, the identification of this specimen was also doubted by Fedosov and Ignatova (2018), who suggested it is apparently close to *Ulota rehmannii.* In addition, Suzuki and Iwatsuki (2013) considered that *Ulota megalospora* is similar to Japanese *U. reptans*, and the latter differs in smooth endostome segments and smaller spores. However, our study shows that the endostome segments of *Ulota reptans* are not always smooth but sometimes finely papillose. In this case, *Ulota reptans* differs from *U. megalospora* in smaller spores (30–38 μm) and indistinct neck of dry capsules, which makes the stomata position apparently at the base rather than the central part of capsules.

In *Ulota*, the leaf length of all species is at least 1 mm, except for a few ones, including *U. gigantospora* from China, *U. macrocalycina* from South America, *U. reptans* from Japan, and *U. megalospora*. The differences between *Ulota reptans* have been mentioned above. *Ulota gigantospora* is segregated from *U. megalospora* by the multicellular spores (87–105 μm), often crisped leaves, and much hairier calyptra, and *U. macrocalycina* is distinguished by the erect-appressed leaves, many hyaline, thin-walled cells at basal leaf margins, strongly constricted capsules, short neck, stomata on the urn and naked calyptra.

The constriction of dry capsules within *Ulota megalospora* varies, from hardly to strongly. The hairiness of calyptra is from sparsely to densely.

Key to *Ulota megalospora* and its closely related species.

1. Spores multicellular, 87–105 μm; leaves variably crisped when dry.. *U. gigantospora*
1. Spores unicellular, 29–51 μm; leaves erect to flexuose when dry........................2
2. Leaves erect-appressed when dry; leaf cells at basal margins distinctly differentiated in 4–10 rows, with thin walls; capsules strongly constricted when dry; stomata confined to the urn; calyptra always naked.............. *U. macrocalycina*
2. Leaves erect to flexuose when dry; leaf cells at basal margins variably differentiated, with only thickened transverse walls; capsules hardly to moderately constricted when dry; stomata located at the base of urn or the junction between urn and neck; calyptra sparsely hairy, sometimes naked.....................3
3. Capsules with short neck when dry; stomata at the base of capsules; seta relatively short, 2.5–3.2 mm; spores relatively small, 30–38 μm............. *U. reptans*
3. Capsules with long neck when dry; stomata at the central part of capsules; seta longer, 3–4.5 mm; spores large, 41–51 μm.................................... *U. megalospora*

Additional Specimens Examined: **Canada**. British Columbia: Calvert Island, 128°6′ W, 51°38′ N, 3 Aug. 1986, *W. B. Schofield 86116* (UBC); Cortes Island, Dawson's Landing, 2 Aug. 1986, *W. B. Schofield 85988-1* (UBC); Floodplain of Squamish River, 22 Apr. 1969, *W. B. Schofield & C. C. Chuang 38764* (UBC); Fraser Canyon, 28 Mar. 1979, *W. B. Schofield 71567* (UBC); Haney Research Forest, 6 Apr. 1978, *W. B. Schofield 68363* (UBC); Jervis Inlet, *W. B. Schofield 63846* (UBC), 24 May 1977, *W. B. Schofield 22624583-1* (UBC); Garibaldi Station, 19 Oct. 1986, *W. B. Schofield 87515* (DUKE); Nelson Creek, 6 Feb. 1978, *W. B. Schofield 67698* (UBC), Sunshine Coast, 8 Aug. 2002, *W. B. Schofield 120067* (UBC); Pitt Island, 21–23 Jun. 1979, *W. B. Schofield 72449* (UBC), 23–25 Jun. 1979, *W. B. Schofield 72795* (UBC); Quadra Island, 23 Jul. 1979, *W. B. Schofield 73697* (UBC); Queen Charlotte Island, 29 Jun. 1971, *W. B. Schofield 44549-2* (DUKE); Queens Reach, 24 May 1977, *W. B. Schofield 22662934* (UBC); Shannon Falls, 22 May 1980, *W. B. Schofield, J. van Velzen & A. Cheung 74842* (UBC); s. loc., 31 Jul. 2000, *L. Baldwin LB1128* (UBC), 3 Aug. 1986, *W. B. Schofield 86116-1* (DUKE), 10 Aug. 1965, *W. B. Schofield 27798-1* (DUKE), 12 Aug. 1969, *R. L. Halbert 42573-1* (DUKE); Trail from Brandywine Falls area toward Brew

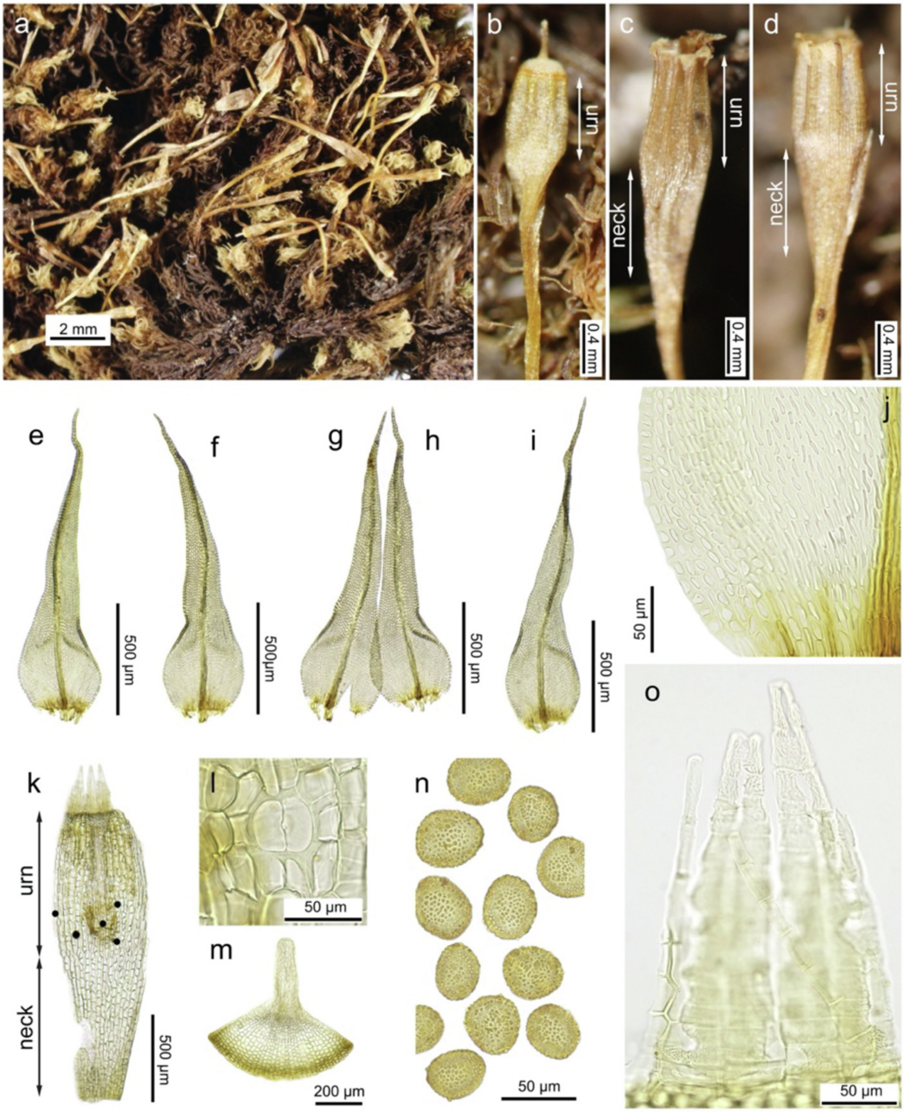


FIG. 117 – *Ulota megalospora* Venturi. a. Habit. b–d. Capsules in dry. e–i. Leaves. j. Marginal cells at leaf base. k. Exothecial wall, with dots indicating stoma position. l. Stoma. m. Operculum. n. Spores. o. Peristome. (All from *W. B. Schofield & J. H. Lyford 72252* [non-type, UBC] except a–d from *W. B. Schofield 72346* [non-type, UBC]).

Lake, 10 Aug. 1974, *W. B. Schofield 56947* (DUKE); Trail to Pierce Lake from Chilliwack Valley, 14 Feb. 1986, *W. B. Schofield & R. J. Belland 84609* (UBC); Vancouver Island, Bamfield, 7 May 1974, *W. B. Schofield 55566-2* (UBC), Brooks Peninsula, 10 Aug. 1984, *W. B. Schofield 82568* (UBC).

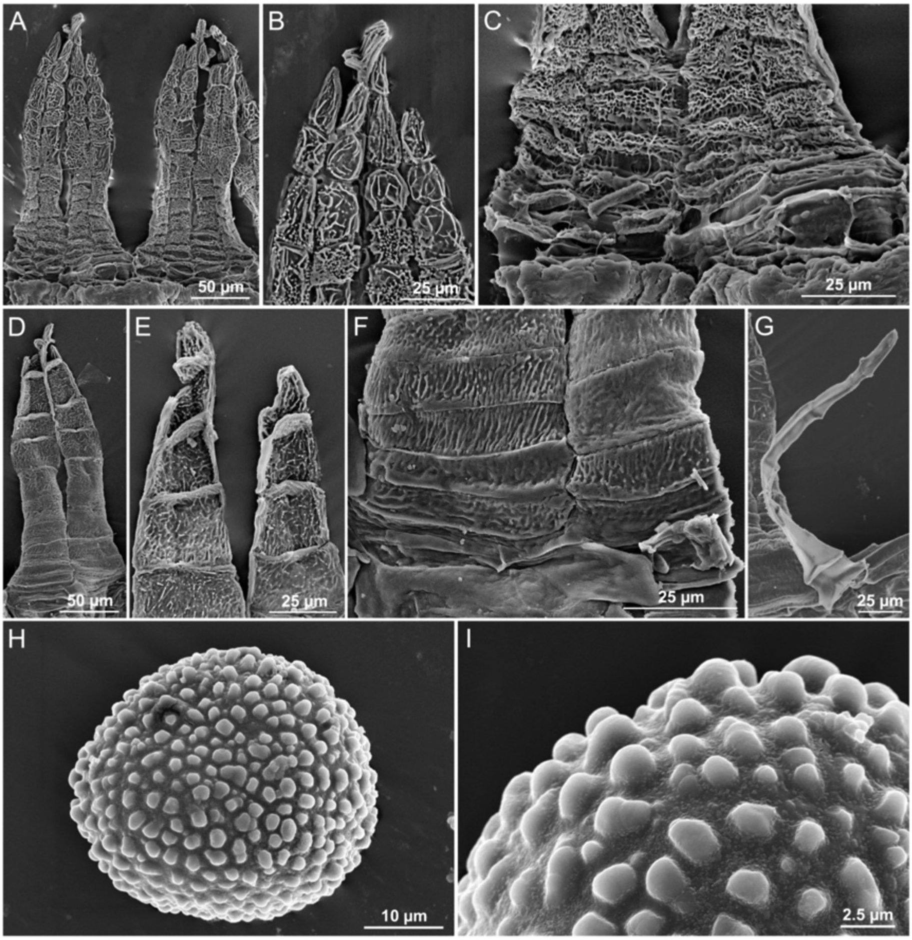


Fig. 118 – *Ulota megalospora* Venturi. A, outer view of exostome; B, outer surface of upper exostome; C, outer surface of basal exostome; D, inner view of exostome; E, inner surface of upper exostome; F, inner surface of basal exostome; G, outer surface of endostome; H, a spore; I, surface ornamentation of a spore. (A–F from *W. B. Schofield & R. J. Belland no.84609* [non-type, UBC], G–I from *D. H. Wagner m2525* [non-type, DUKE]).

U.S.A. Alaska: Latouche Island, 29 Jul. 1957, *H. T. Shacklette 4721* (MICH); Mitkof Island, 23 Jun. 1968, *I. A. Worley & W. B. Schofield 8643* (UBC), 22 Jun. 1968, *s.coll.* (UBC); Yakutat, 4 Feb. 1846, *H. S. Mazaika 5120* (MICH), 13 Jul. 1845, *L. D. Stair 5045* (MICH), 2 Jun. 1846, *H. S. Mazaika 5119* (MICH). California: Humboldt Co., 8 Jun. 1973, *D. H. Norris 24304* (H); Del Norte Co., 5 Apr. 1989, *D. H. Norris 74144* (UC), *74145* (UC); Trinity Co., Jun. 1986, *D. H. Norris 72572b* (H). Oregon: Benton Co., 30 Jul. 2009, *D. H. Wagner m2525* (DUKE); Clatsop Co., 5 Jun. 1979, *W. B. Schofield & J. H. Lyford 72252* (UBC); Linn Co., 6 Feb. 1993, *D. H. Norris 80482* (H, UC); Marion Co., 6 Jun. 1997,

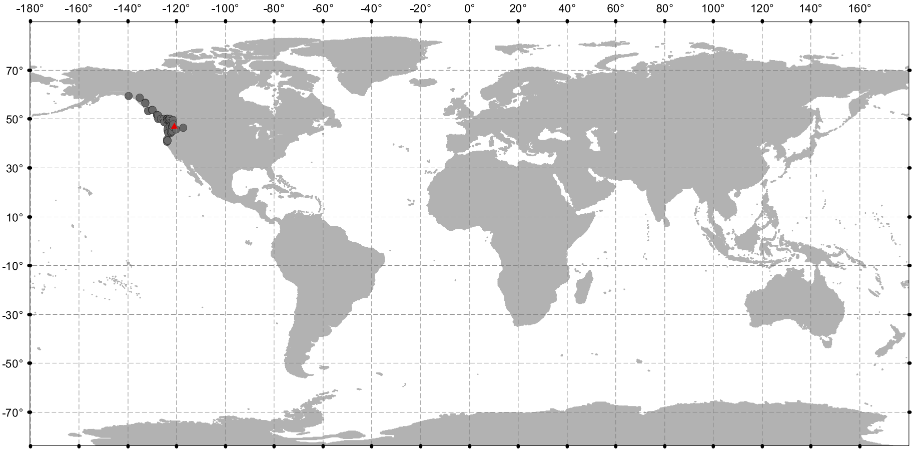


FIG. 119 – Distribution of *Ulota megalospora* worldwide. The red triangle indicates the type locality.

D. H. Wagner 8746 (DUKE); Mt. Hebo, 6 Jun. 1979, *W. B. Schofield 72346* (DUKE, UBC). WASHINGTON: Cascade Mt., 3 Jul. 1898, *J. A. Allen 81* (DUKE, H, MICH); Clallam Co., 31 Jul. 1962, *R. R. Ireland, Jr. 6362* (MICH); Lewis Co., 3 May 2000, *W. B. Schofield 114345* (UBC); Pierce Co., 28 Aug. 1969, *F. J. Hermann 22726* (DUKE), Fairfax, 11 Aug. 1923, *J. W. Bailey s.n.* (MICH); Scagit Co., 18 Feb. 1983, *W. B. Schofield 78876* (UBC); Skamania Co., 11 Apr. 2002, *W. B. Schofield 119388* (UBC); Snohomish Co., 29 May 1977, *E. Lawton 5850* (DUKE), 12 Jul. 1966, *E. Lawton 5639* (H), 23 Oct. 2002, *W. B. Schofield 120610* (UBC), 2 Jul. 1963, *F. J. Hermann 18498* (MICH), 13 Aug. 1931, *s.coll.* (MICH).

31. **ULOTA MEMBRANATA** Malta, Acta Horti Bot. Univ. Latv. 7: 18. 3. 1933. TYPE: AUSTRALIA. Tasmania, West coast, Comet-Dundas Road, on wood, 17 Oct. 1893, *W. A. Weymouth 1652* (holotype, H4336011! isotypes, HO! TR).

Plants 0.8–1.5 cm tall, yellow to green above, brown to black below. Stems usually branched. Leaves erect, flexuose, rarely crisped when dry, patent when moist, (1.2–) 1.5–1.8 (–1.9) mm long; leaf lamina lanceolate, unistratose; leaf base wide, ovate; apex acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, oblong, (3–) 7–10 (–14) × (5–) 7–9 (–10) μm, thick-walled, with low papillae; basal inner cells linear, rectangular, elongate-rectangular to vermicular, (12–) 21–30 (–43) × (1–) 2–3 (–4) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in (2–) 4–6 (–9) rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves are somewhat longer, 2–2.2 (–2.4) mm. Vaginula naked. Seta (2.7–) 3–4.6 (–5) mm long, twisted anticlockwise when dry. Capsule long exserted, 1.5–1.7 (–1.8) mm long. Urn obovoid, ovate-cylindrical or short-cylindrical, slightly to strongly constricted below the mouth when dry and empty, eight furrows along the entire length, with prominent ribs alternately. Neck somewhat long, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, usually four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between the urn and neck, rarely at the lower part of the urn. Preperistome sometimes seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, sometimes lying on the exothecium, lanceolate, densely and finely papillose outside, papillose to striate-papillose inside. Endostome segments 16, lanceolate to wide-lanceolate, ≥1/2 length of teeth, uniseriate or biseriate, at least 1/2 width of teeth, hyaline, smooth outside, almost smooth, slightly scabrous or striate inside. Opercula with a short to medium-long beak. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, very large, multicellular, (70–) 84–105 (–121) μm in diameter.

Illustration: Malta (1933), Sainsbury (1955) and Ramsay (2006); figures 120 and 121.

Habitat: It grows on trees, such as *Dracophyllum*. There are some records of altitude: (765–) 1067–1524 (–1676) m. It occasionally grows mixed with *Ulota crispa*.

Distribution: It occurs in New Zealand, rarely in Tasmania in Australia. Figure 122.

Notes: *Ulota membranata* was named by Malta (1927) according to its preperistome, which was described as "a somewhat irregular, slightly striated membrane". This is the first, but not the only, report of preperistome in the genus *Ulota*. During our study, preperistome occasionally appeared in other species, such as *Ulota angusti-limbata*, *U. curvifolia*, *U. delicata*, and *U. magellanica*.

Ulota membranata is characteristic of non-crisped leaves, ovate-cylindrical dry capsules, 16 wide endostome segments, and multicellular spores. The Chinese *Ulota latisegmenta* and the South American *U. billbuckii* and *U. magellanica* also have 16 wide endostome segments, but these species differ in hardly or weakly differentiated cells at basal leaf margins (often ≤4 rows) and cylindrical capsules, and the strongly crisped leaves in *Ulota latisegmenta* and the sparsely hairy to naked calyptra in *U. magellanica*.

In *Ulota*, species with multicellular spores are rare, and their morphological differences have been discussed in a previous study (Garilleti *et al.*, 2012) and this work (see Notes in *U. gigantospora*). Among them, *Ulota membranata* is the most similar to *U. billbuckii* from South America. In both, the leaves are non-crisped when dry, and endostome segments are 16 and wide. However, *Ulota billbuckii* differs in hardly differentiated cells at basal leaf margins (often one row), cylindrical capsules with short neck, and strongly constricted when dry.

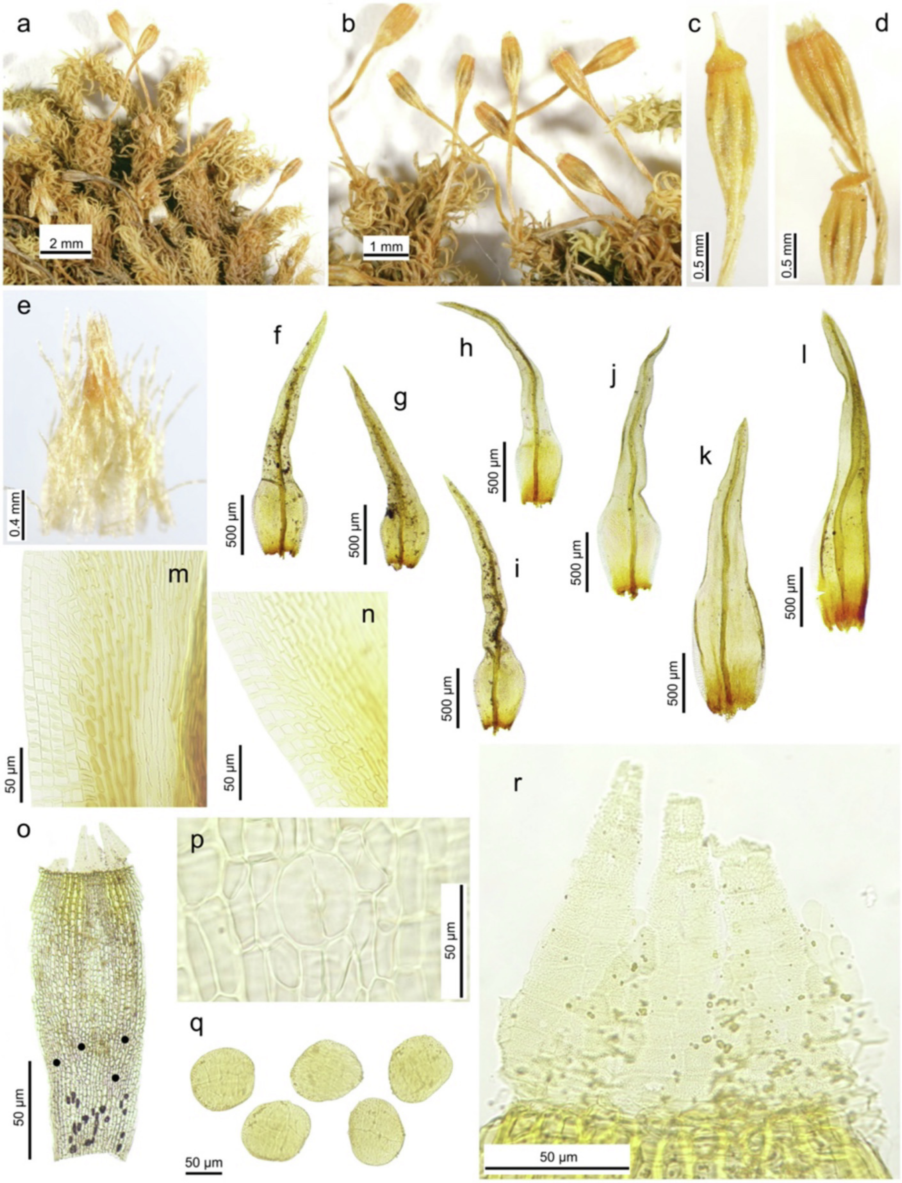


FIG. 120 – *Ulota membranata* Malta. a–b. Habit. c–d. Capsules in dry. e. Calyptra. f–j. Leaves. k–l. Perichaetial leaves. m–n. Marginal cells at leaf base. o. Exothecial wall, with dots indicating stoma position. p. Stoma. q. Spores. r. Peristome. (a–l from *W. A. Weymouth 22* [non-type, HO], m–r from *L. Vish 113* [non-type, H]).

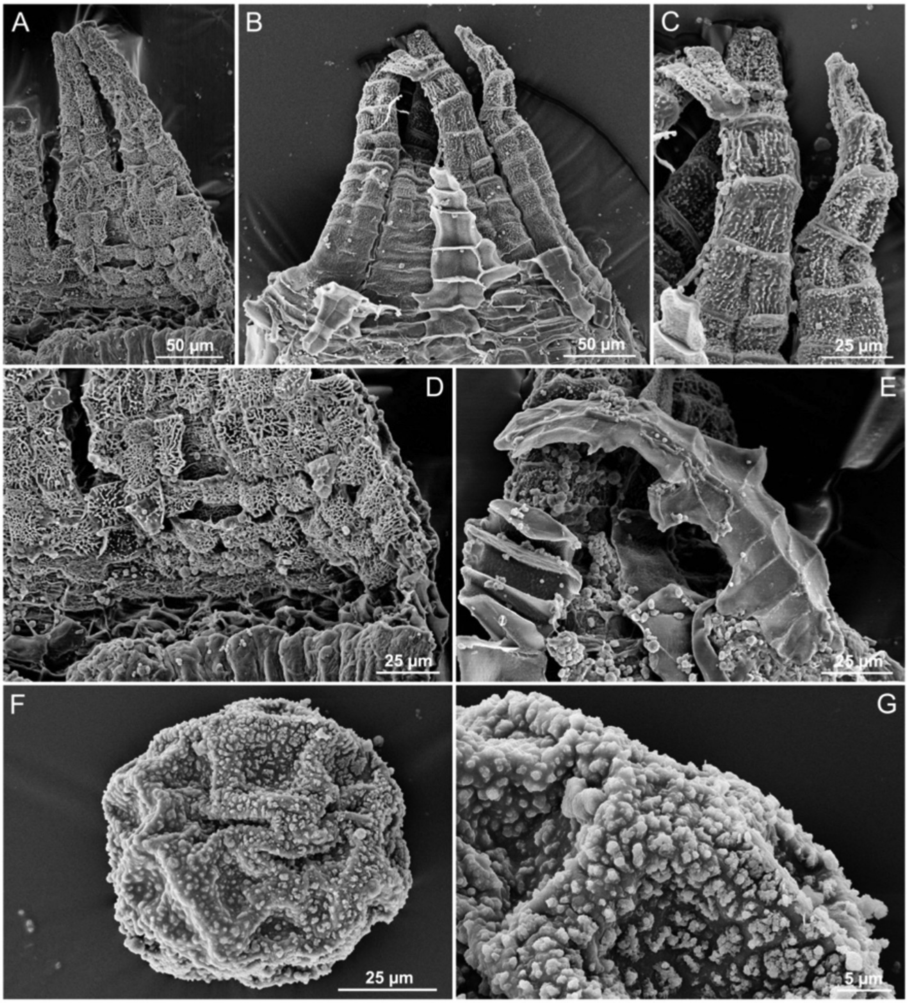


FIG. 121 – *Ulota membranata* Malta. A, outer view of exostome; B, inner view of peristome; C, inner surface of upper exostome; D, outer surface of basal exostome; E, outer surface of endostome; F, a spore; G, surface ornamentation of a spore. (All from *G. O. K. Sainsbury 348* [non-type, S] except A, D and E from the isotype in HO).

Key to *Ulota membranata* and its closely related species.

1. Spores unicellular, 20–44 μm..2
1. Spores multicellular, 84–105 μm..3
2. Leaves strongly crisped when dry; leaf cells at basal margins somewhat differentiated, 2–4 rows; capsules relatively large, 2–2.6 mm long; calyptra densely hairy; spores relatively small, 20–35 μm.......................... *U. latisegmenta*

2. Leaves erect, sinuose, and falcate when dry; leaf cells at basal margins hardly differentiated, ≤3 rows; capsules small, 1–1.4 mm long; calyptra sparsely hairy to naked; spores large, 36–44 μm................................ *U. magellanica*
3. Leaf cells at basal margins hardly differentiated, often one row; capsules cylindrical, with short neck that abruptly narrowed to the seta, strongly constricted when dry.. *U. billbuckii*
3. Leaf cells at basal margins distinctly differentiated, 4–6 rows; capsules obovate to ovate-cylindrical, with slightly long neck that gradually narrowed to the seta, variably constricted when dry.. *U. membranata*

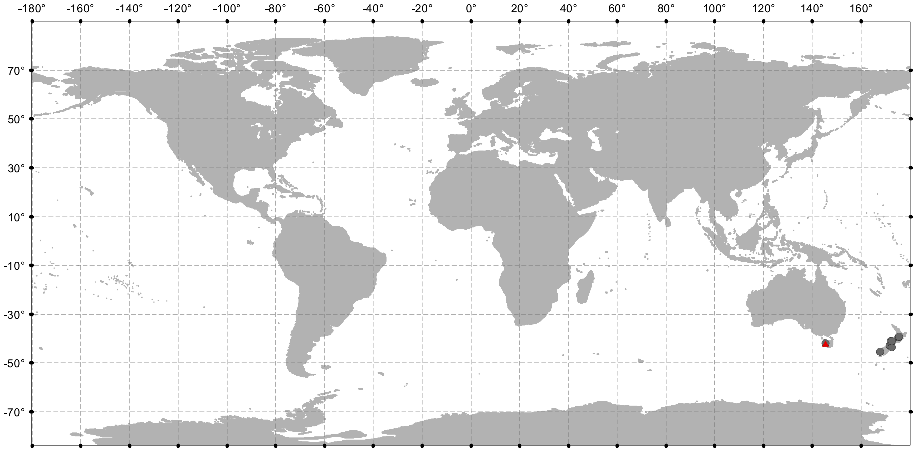


FIG. 122 – Distribution of *Ulota membranata* worldwide. The red triangle indicates the type locality.

Additional Specimens Examined: **Australia**. TASMANIA: West Coast, 17 Oct. 1893, *W. A. Weymouth 21* (BM); south of Narcissus Hut, 14 Jan. 2004, *K. Felton s.n.* (HO).

New Zealand. CANTERBURY: s. date, *L. Vish 113* (H), 30 Dec. 1935, *G. O. K. Sainsbury 5086* (CHR). MANAWATU-WANGANUI: Mt. Ruapehu, 6 Nov. 1925, *R. Mundy 116* (CHR), Jan. 1939, *G. O. K. Sainsbury s.n.* (HBG, MICH), *348* (S), 27 May 1987, *J. E. Braggins 87/59* (AM). SOUTHLAND: Fiordland, 18 Apr. 2002, *C. Newell s.n.* (CHR). TASMAN: Golden Bay Co., *J. K. Bartlett s.n.-2* (AM-AK189272–74).

32. **ULOTA MORRISONENSIS** Horik. & Nog., J. Sci. Hiroshima Uni., Ser. B, Div. 2 (Bot.) 3: 37. 1. 1937. TYPE: CHINA. Taiwan, Tainan, Mt. Yushan (Japanese name: Mt. Niitaka), alt. ca. 3300 m, 19 Aug. 1932, *A. Noguchi 5985* (holotype, HIRO; isotype, NICH!).

Plants up to 1.5 cm tall, yellow to green above, dark brown to black below. Stems usually branched. Leaves strongly crisped when dry, patent when moist, (1.9–) 2.5–4.1 (–4.4) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex long acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, hexagonal and oblong, (13–) 15–18 (–20) × (7–) 8–9 (–11) μm, thick-walled, often with low simple papillae; basal inner cells linear, elongate-rectangular to vermicular, (31–) 42–50 (–61) × (5–) 8–11 (–13) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in 3–6 rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves are somewhat longer, (3.8–) 4–4.7 (–4.8) mm. Vaginula not seen. Seta (5.1–) 5.3–7 (–7.3) mm long, twisted anticlockwise when dry. Capsule long exserted, ca. 2.5 mm long. Urn long-cylindrical, more or less constricted below the mouth when dry and empty, with eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the base of the urn or the junction between the urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, variably recurved when dry, lanceolate, and densely papillose on both sides. Endostome segments 16, linear-lanceolate, almost as tall as exostome teeth, uni- or bi-seriate, hyaline, variably incurved when dry, smooth on the outside surface, finely papillose on the inside surface. Opercula usually with a long beak. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (22–) 24–27 (–29) μm in diameter.

Illustration: Noguchi (1937) and Wang and Jia (2012a); figures 123 and 124.

Habitat: It was only recorded as growing on branches of *Pleioblastus* in the protologue. There is only one record of altitude: 3300 m. No mixed growth has been found in this study.

Distribution: It is **endemic** to Taiwan of China. Figure 125.

Notes: *Ulota morrisonensis* and *U. crispa* are the only two species of *Ulota* hitherto reported from Taiwan (Nakanishi, 1963; Noguchi, 1937). The morphology of *Ulota morrisonensis* was discussed thoroughly in a recent study (Wang and Jia, 2018b), therefore we only give a key here to distinguish *U. morrisonensis* from its close species, *i.e.*, *U. crispa*, *U. crispula*, and *U. intermedia*. The basal membrane between endostome segments was illustrated in the protologue (Noguchi, 1937) as very high, but we do not see a distinct basal membrane in the type materials. Recently, Suzuki and Iwatsuki (2013) reported *Ulota morrisonensis* from Japan, but its leaf length (2.3–2.8 mm), seta length (1.5–1.8 mm), smooth endostome segments and spore size (18–23 μm) are obviously different from those of Taiwan's populations. Therefore, we cannot confirm the occurrence of this species in Japan before we examine the collection they used.

There are too few materials of *Ulota morrisonensis* in this study, and thus its variation is unknown

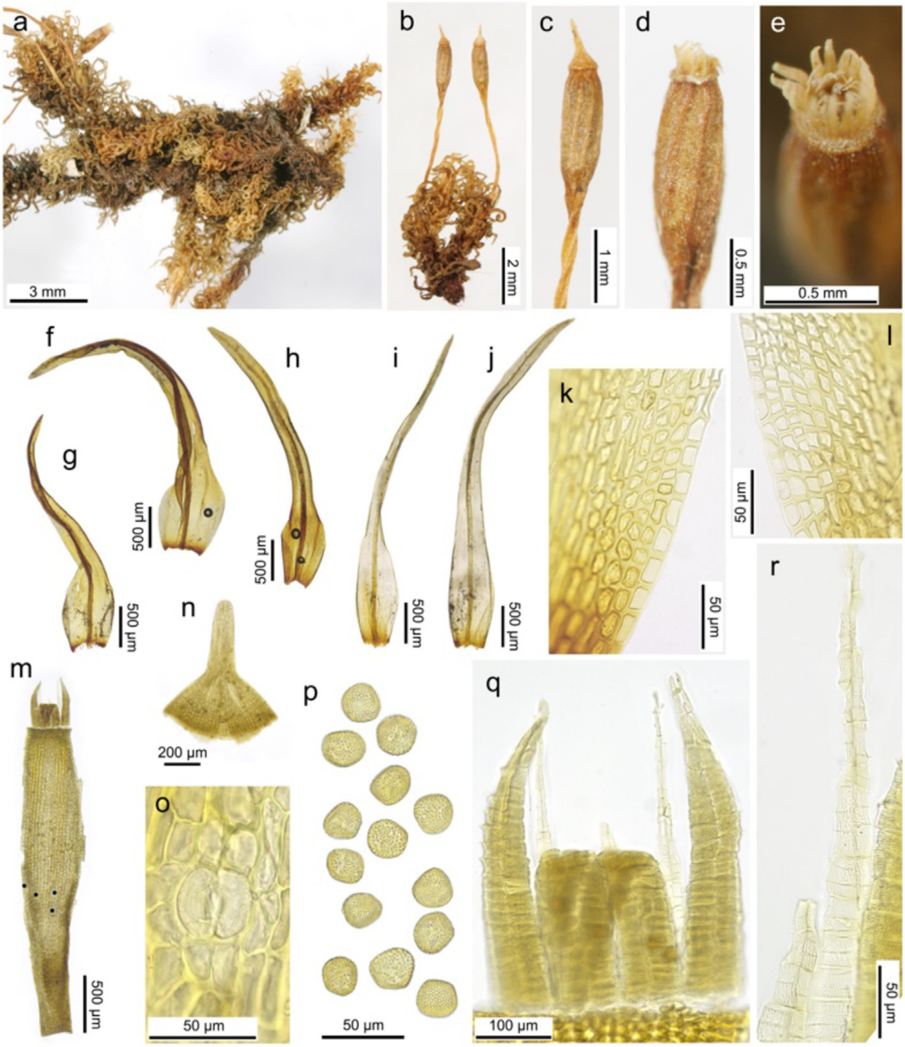


FIG. 123 – *Ulota morrisonensis* Horik. & Nog. a–b. Habit. c–d. Capsules in dry. e. Capsule mouth viewed from above. f–h. Leaves. i–j. Perichaetial leaves. k–l. Marginal cells at leaf base. m. Exothecial wall, with dots indicating stoma position. n. Operculum. o. Stoma. p. Spores. q. Peristome. r. Endostome segments. (All from the isotype in NICH).

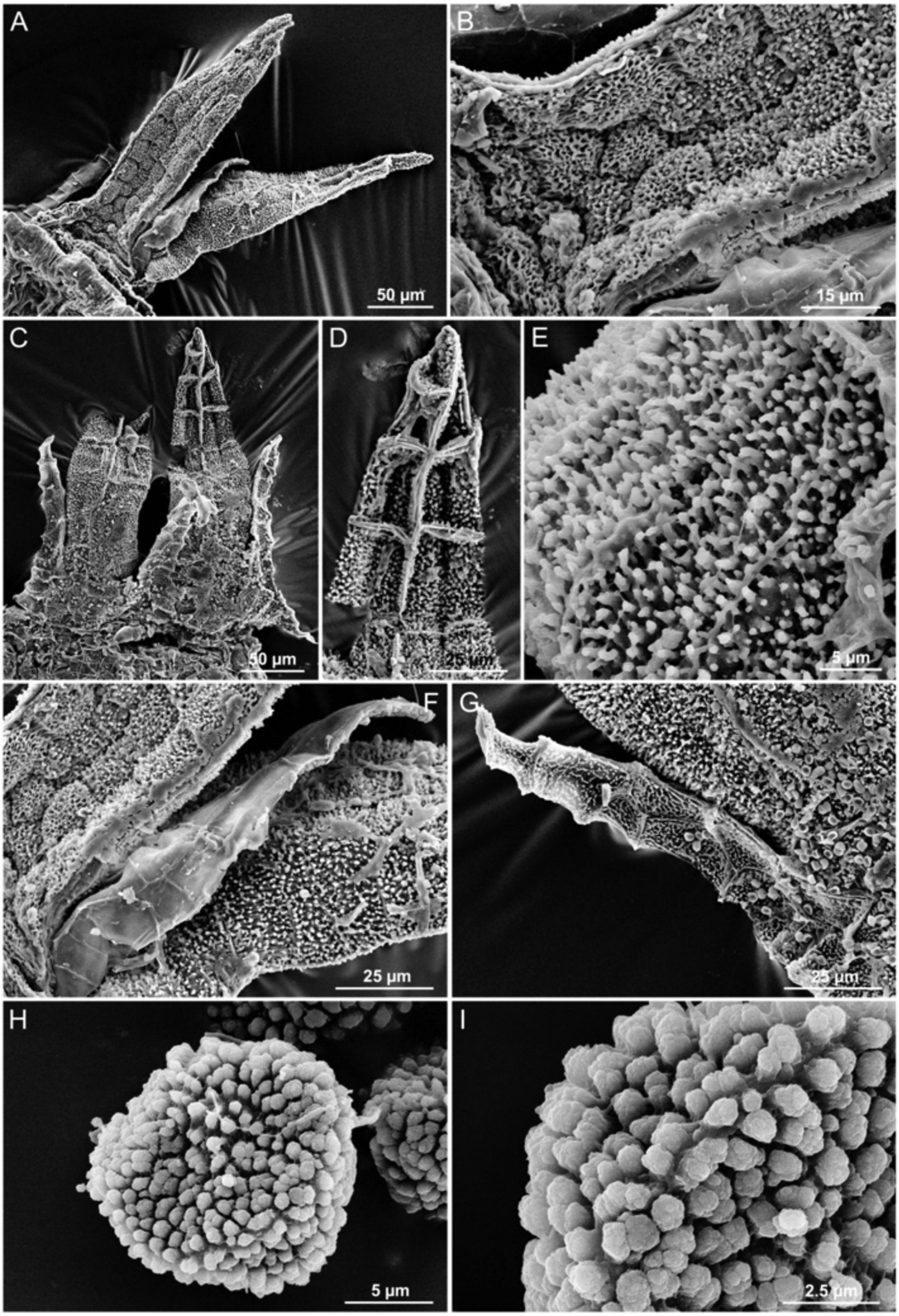


FIG. 124 – *Ulota morrisonensis* Horik. & Nog. A, outer view of exostome; B, outer surface of basal exostome; C, inner view of peristome; D, inner surface of upper exostome; E, inner surface of middle exostome; F, outer surface of endostome; G, inner surface of endostome; H, a spore; I, surface ornamentation of a spore. (All from the isotype in NICH).

Key to *Ulota morrisonensis* and its closely related species.

1. Endostome segments 16; leaves longer, 2.5–4.1 mm; leaf cells at basal margins differentiated in less rows (3–6); endostome segments finely papillose inside; seta longer, 5.3–7 mm......*U. morrisonensis*
1. Endostome segments 8, rarely up to 16; leaves relatively shorter, 2.1–3 mm; leaf cells at basal margins often differentiated in more rows (4–11); endostome segments slightly scabrous to nearly smooth inside; seta relatively shorter, 2–5 mm......2
2. Capsules cylindrical to long-cylindrical, strongly constricted when empty and dry; endostome segments 8, rarely up to 16, narrow-lanceolate; leaves always strongly crisped when dry......*U. crispa*
2. Capsules cylindrical to short cylindrical, not or slightly constricted when empty and dry; endostome segments 8, linear to linear-lanceolate, sometimes fragile and slender; leaves slightly to strongly crisped when dry......3
3. Leaves flexuous, slightly to moderately crisped when dry; endostome segments linear, often fragile......*U. crispula*
3. Leaves strongly crisped when dry; endostome segments linear-lanceolate, not fragile......*U. intermedia*

Additional Specimens Examined: **China**. Taiwan: Mt. Notaka, 9 May 1919, *K. Sawada s.n.* (TNS).

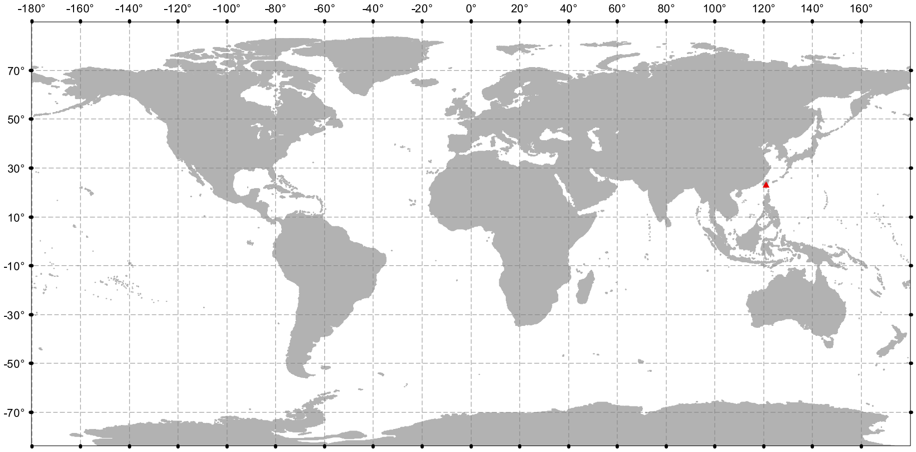


Fig. 125 – The type locality of *Ulota morrisonensis.*

33. **Ulota novo-guinensis** E.B. Bartram, Brittonia 11: 91. 1959. Type: Papua New Guinea. Eastern Highlands, Chimbu sub-district, above Lake Punda, e slope Mt. Wilhelm, on branches of small tree, alt. ca. 3950 m, 24 Jul. 1956, *R. D. Hoogland & R. Pullen 5765* (holotype, FH00079856! L.0060831!).

Plants 0.7–1.7 cm tall, yellow to green above, brown to black below. Stems usually branched. Leaves strongly crisped, rarely flexuose when dry, patent when moist, (1.7–) 1.9–2.1 (–2.2) mm long; leaf lamina lanceolate, unistratose; leaf base wide, ovate; apex acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, oblong, (8–) 10–13 (–16) × (7–) 9–11 (–13) μm, thick-walled, with low papillae; basal inner cells linear, rectangular, elongate-rectangular to vermicular, (23–) 29–40 (–53) × (3–) 4–5 (–7) μm, with strongly thickened wall, smooth; basal marginal cells weakly differentiated, only one, rarely two rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves much longer, (2.3–) 2.7–3.1 (–3.3) mm. Vaginula not seen. Seta ca. 4 mm long, twisted anticlockwise when dry. Capsule long exserted, ca. 1.5 mm long. Urn cylindrical to short-cylindrical, strongly constricted below the mouth when dry and empty, often forming bottleneck just beneath the mouth, eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly or gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, usually four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, often lying on the exothecium, lanceolate, densely papillose on the outside, finely papillose above and nearly smooth below on the inside. Endostome segments 16, linear, as long as teeth, uniseriate or partially biseriate, about 1/3 width of teeth, hyaline, (almost) smooth on both sides. Opercula with a medium-long beak. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, very large, multicellular, (95–) 110–125 (–140) μm in diameter.

Illustration: Vitt *et al.* (1993); figures 126–128.

Habitat: It grows on trunks or twigs of trees or shrubs, but no phorophyte was recorded. There are a few records of altitude: 3500–3950 m. No mixed growth has been found in this study.

Distribution: It is **endemic** to Papua New Guinea. Figure 129.

Notes: *Ulota novo-guinensis* is easily distinguished by the strongly crisped leaves, hardly differentiated cells at basal leaf margins, often short-cylindrical capsules, 16 narrow endostome segments, and multicellular spores.

In *Ulota*, species with multicellular spores are rare, and their morphological differences have been discussed in a previous study (Garilleti *et al.*, 2012) and the present work (see Notes in *U. gigantospora*). Among them, *Ulota novo-guinensis* is similar to *U. gigantospora* from China. Besides multicellular spores, they also often have crisped leaves, weakly differentiated cells at basal leaf margins, short capsules, narrow endostome segments, and densely calyptra. However, *Ulota gigantospora* differs in having smaller leaves (1.1–1.7 mm) with a rounded base and eight endostome segments with obscurely papillose inside.

Additionally, *Ulota novo-guinensis* is also close to *U. morrisonensis* from Taiwan in China. They share in strongly crisped leaves and 16 narrow endostome segments, but *Ulota morrisonensis* is distinguished by more rows (3–6) of hyaline cells at basal leaf margins, long-cylindrical capsules, and unicellular spores (24–27 μm).

No noteworthy variation within *Ulota novo-guinensis* was seen.

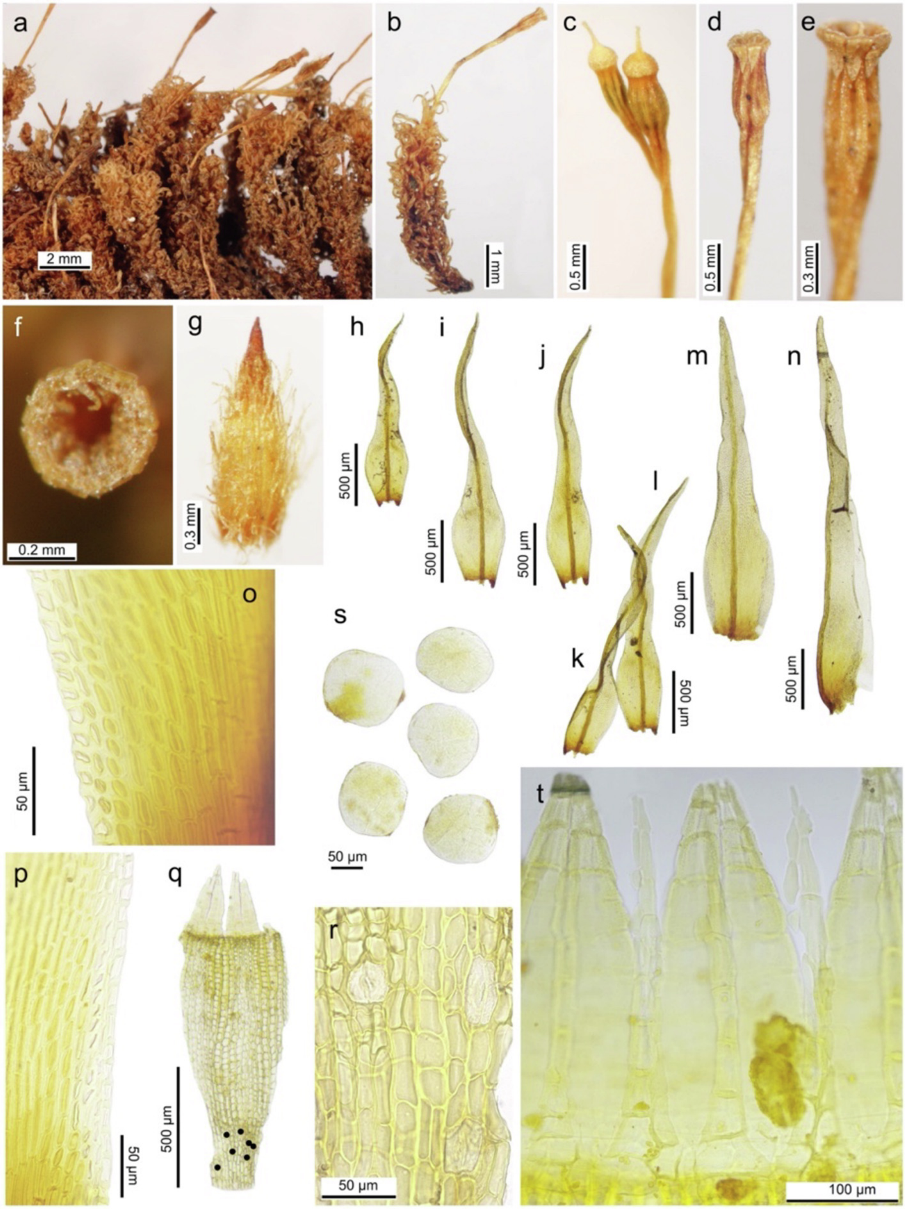


FIG. 126 – *Ulota novo-guinensis* E.B. Bartram. a–b. Habit. c–e. Capsules in dry. f. Capsule mouth viewed from above, with endostome segments mostly fallen. g. Calyptra. h–l. Leaves. m–n. Perichaetial leaves. o–p. Marginal cells at leaf base. q. Exothecial wall, with dots indicating stoma position. r. Stomata. s. Spores. t. Peristome. (All from the holotype in FH).

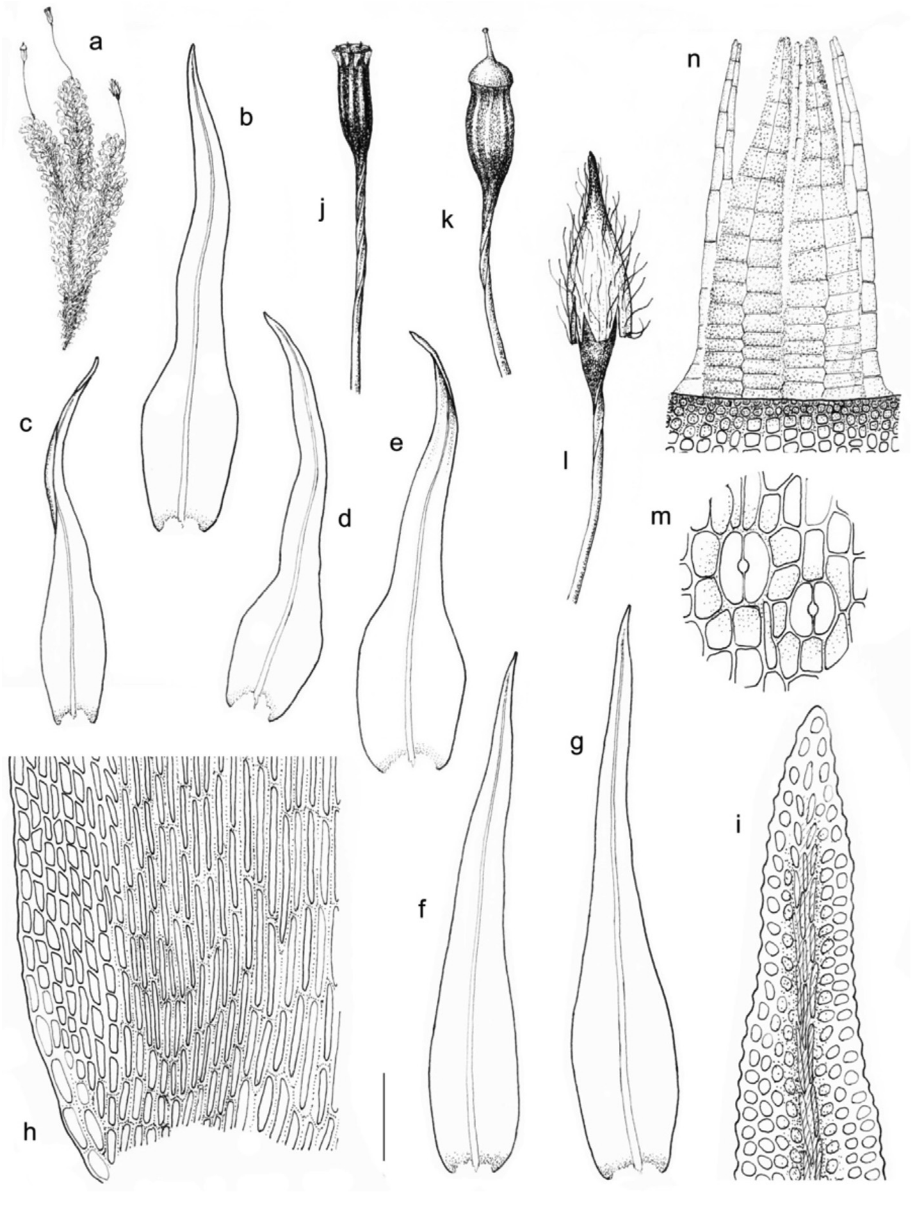


FIG. 127 – *Ulota novo-guinensis* E.B. Bartram. a. plant; b–e. leaves; f–g. perichaetial leaves; h. basal marginal cells; i. top laminal cells; j. an empty capsule in dry; k. a capsule with operculum; l. a capsule with calyptra; m. stomata; n. a portion of peristome. (Scale bar: a, 10 mm; f and g, 0.5 mm; h, i, m, 0.05 mm; j–l, 1.0 mm; n, 0.1 mm. All drawn from holotype in FH).

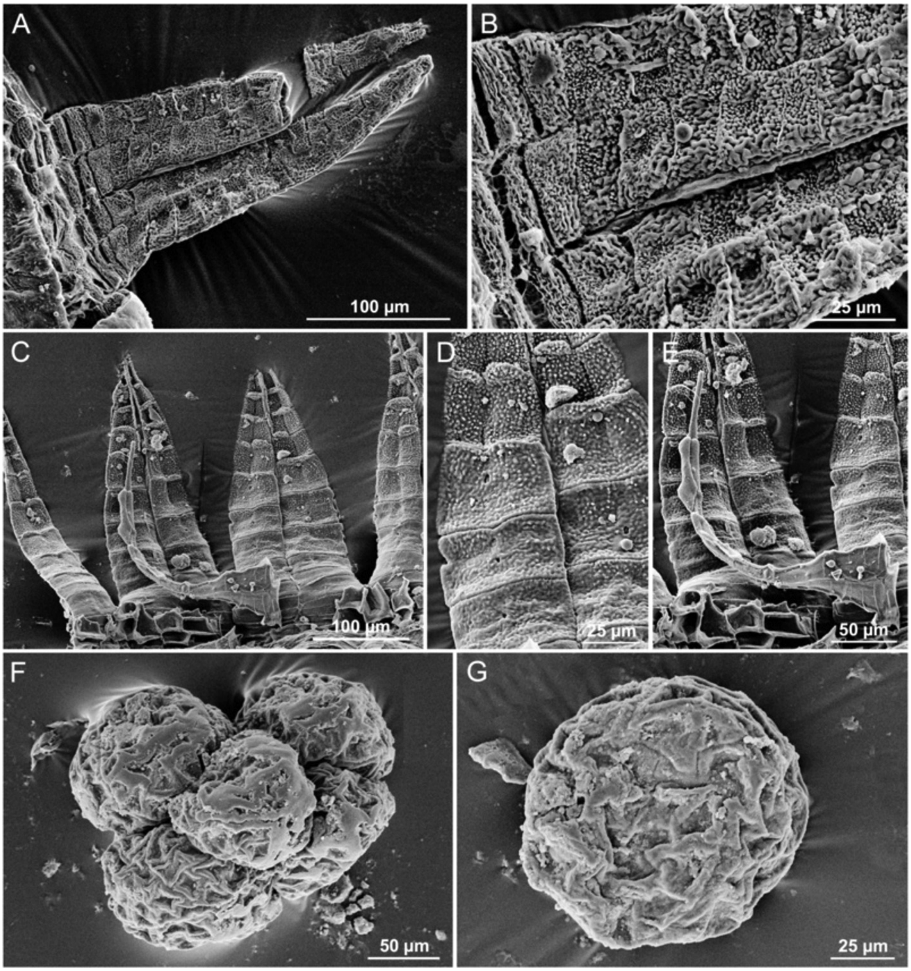


FIG. 128 – *Ulota novo-guinensis* E.B. Bartram. A, outer view of exostome; B, outer surface of basal exostome; C, inner view of peristome; D, inner surface of upper exostome; E, inner surface of endostome; F, spores; G, surface ornamentation of a spore. (All from the holotype in FH).

Key to *Ulota novo-guinensis* and its closely related species.

1. Spores unicellular, 24–27 μm; leaf cells at basal margins differentiated in 3–6 rows; capsules long-cylindrical.. *U. morrisonensis*
1. Spores multicellular, 87–125 μm; leaf cells at basal margins hardly differentiated, no more than 3 rows; capsules cylindrical to short-cylindrical...................2
2. Endostome segments 8, obscurely papillose inside; leaves smaller, 1.1–1.7 mm, with rounded; spores relatively small, 87–105 μm..................... *U. gigantospora*
2. Endostome segments 16, smooth inside; leaves longer, 1.9–2.1 mm, with ovate; spores large, 110–125 μm.. *U. novo-guinensis*

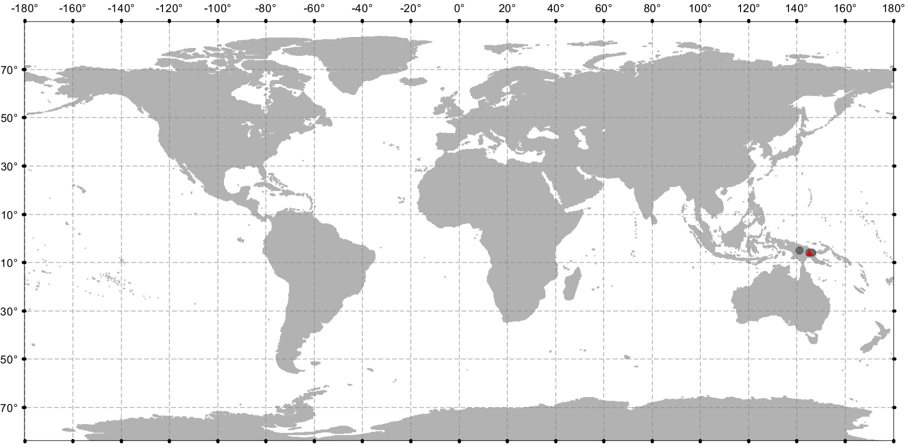


FIG. 129 – Distribution of *Ulota novo-guinensis* worldwide. The red triangle indicates the type locality.

Additional Specimens Examined: **Papua New Guinea**. EASTERN HIGHLANDS: Mt. Wilhelm, 27 Feb. 1965, *A. Eddy 2501* (BM000844911–12). MADANG: Mt. Abilala, 19 Nov. 1964, *A. Eddy 1252* (BM). WEST SEPIK: Star Mts., 15 Apr. 1975, *A. Touw 16274-2* (H), 27 Apr. 1975, *16870* (H, L).

34. **ULOTA OBTUSIUSCULA** Müll. Hal. & Kindb., Cat. Canad. Pl., Musci 82. 1892. ≡ *Orthotrichum obtusiusculum* (Müll. Hal. & Kindb.) Kindb., Eur. N. Amer. Bryin. 2: 307. 1897. TYPE: CANADA. British Columbia, on small maple trees in thickets along the Coquihalla River near New Westminster Junction, 26 Apr. 1889, *J. Macoun* (isolectoypes, NY00524157! designated here; isolectotype, BM000982367–69! FH! MO! NY00524156!); Vancouver Island, Fort Rupert, 1885, *Dawson* (paralectotypes, NY00524154! CANM).

Ulota alaskana Cardot & Thér., Proc. Wash. Acad. Sci. 4: 309. 15 f. 4. 1902. ≡ *Ulota crispa* var. *alaskana* (Cardot & Thér.) Grout, Moss Fl. N. Amer. 2: 134. 1935. TYPE: U.S.A. Alaska, Point Gustavus, Glacier Bay, 6 Oct. 1899, *Coville and Kearney no.774* (lectotype, PC0099344! isotype, S-B181073!); Wrangell, 5 Jun. 1899, *Coville and Kearney no. 407* (paratypes, BM000982371! MO1950008! S-B181074!).

Plants 1–3.5 cm tall, yellow to green above, brown to dark brown below. Stems usually branched. Leaves strongly crisped when dry, patent when moist, (2.4–) 2.8–3.7 (–4.1) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded, concave; apex long acuminate; leaf margin plane, sometimes partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (8–) 9–11 (–14) × (7–) 8–10 (–11) μm, thick-walled, with low papillae; basal inner cells linear, rectangular, elongate-rectangular to vermicular, (23–) 33–45 (–61) × (1–) 2–5 (–8) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in (1–) 3–7 (–10) rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves much longer, (3.3–) 3.4–4.6 (–4.8) mm. Vaginula is sparsely hairy. Seta (3–) 5–7.5 (–9) mm long, often twisted anticlockwise when dry. Capsule long exserted, (1–) 1.3–2 (–2.3) mm long. Urn cylindrical to long-cylindrical, hardly or slightly constricted below the mouth when dry and empty, eight furrows along the entire length, with prominent ribs alternately. Neck long when the capsule is dry and empty, gradually narrowed to the seta. Exothecial cells near the mouth, sometimes red or orange, and also distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between the urn and neck or the central part of capsules. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, often lying on the exothecium, lanceolate, densely papillose on the outside, striate above and smooth below on the inside. Endostome segments 8, narrow-lanceolate, almost as long as the teeth, uniseriate or partially biseriate, 1/2–1/3 width of teeth, hyaline, smooth outside, slightly scabrous inside. Opercula usually with a short to long beak. Calyptra mitrate, densely, rarely sparsely hairy. Spores spherical, finely papillose, (24–) 27–30 (–34) μm in diameter.

Illustration: Figures 130 and 131.

Habitat: It grows on trunks and branches of trees, such as apples, birch, *Alnus* (alder), and *Rhamnus*. There are some records of altitude: (0–) 15–110 (–244) m. It is occasionally mixed with *Ulota crispa* and *U. drummondii*.

Distribution: It is common on the west coast of North America. Figure 132.

Notes: *Ulota obtusiuscula* is an unusual species in the genus with large plant size and very long seta. Moreover, the capsules with a long neck and hardly constricted when dry is another prominent character of this species (Vitt, 2014; Müller and Kindberg, 1892).

Ulota obtusiuscula resembles *U. crispa* in having strongly crisped leaves, distinctly differentiated cells at basal leaf margins, long exserted capsules, eight narrow endostome segments, and densely hairy calyptra. However, *Ulota crispa* is distinguished by the relatively small plant (0.5–2.5 cm), more rows (5–11) of hyaline cells at basal leaf margins, moderately to strongly constricted capsules without red or orange cells near the mouth, and relatively shorter seta (3–5 mm). In North America, Vitt (2014) considered that *Ulota obtusiuscula* was confined to the west coast while *U. crispa* is restricted to the eastern half of the continent. This is generally confirmed by our present study, but whether the small amount of *Ulota crispa* reported from the west coast are the young plants of *U. obtusiuscula*, as Vitt stated (2014), still needs further study.

Outside North America, *Ulota obtusiuscula* seems related to *U. splendida* from Papua New Guinea. They share in large plants, strongly crisped leaves, very long seta, eight narrow-lanceolate endostome segments, and densely hairy calyptra. However, in *Ulota splendida* the leaf cells at basal margins are hardly differentiated, and capsules are longer (2–3.2 mm) and strongly constricted when dry.

No noteworthy variation within *Ulota obtusiuscula* was seen.

Key to *Ulota obtusiuscula* and its closely related species.

1. Leaf cells at basal margins hardly differentiated; capsules long, 2–3.2 mm; leaves arranged relatively sparsely on stems and branches........................*U. splendida*
1. Leaf cells at basal margins differentiated in 3–11 rows; capsules relatively short, 1.3–2.2 mm; leaves arranged densely on stems and branches...........................2
2. Plant relatively small, 0.5–2.5 cm; leaf basal marginal cells differentiated in more rows (5–11); capsules moderately to strongly constricted when dry; exothecial cells near mouth never red or orange; seta relatively short, 3–5 mm..*U. crispa*
2. Plant large, 1–3.5 cm; leaf basal marginal cells differentiated in 3–7 rows; capsules hardly or slightly constricted when dry; exothecial cells near mouth sometimes red or orange; seta long, 5–7.5 mm.........................*U. obtusiuscula*

Additional Specimens Examined: **Canada**. British Columbia: Delta of Goodspeed River at the end of Holberg Inlet. Grassy flats, 128°0′ W, 50°39′ N, 26 Jul. 1967, *G. F. Otto 1903* (UBC); Digby Island, 13 Nov. 1964, *F. M. Boas 36-1* (UBC); "Ronning's Palce" appr. 8 mi W. of Holberg, 128°02′ W, 53°40′ N, 25 Jul. 1967, *G. F. Otto 1839M* (UBC), *1844M* (UBC); Golden Ears Provincial Park, 122°30′ W, 49° 20′ N, 25 Jun. 2003, *W. B. Schofield 121319* (UBC); Prince Rupert Area, 24 Jun. 1979, *D. H. Vitt and D. G. Horton s.n.* (H, MICH); Queen Charlotte Island, 132°30′ W, 53°08′ N, 9–12 Jul. 1962, *W. B. Schofield & F. M. Boas 18736* (H, MICH, PE), 132°09′ W, 53°50′ N, 18 Jun. 2002, *W. B. Schofield 119612* (UBC), 21 Jun. 2002, *119812* (DUKE, UBC), Kootenay Inlet, 132°15′ W, 52°50′ N, 10 Jul. 1966, *W. B. Schofield 31152* (H), Graham Island, 132°55′ W, 53°35′ N, 6–10 Jun. 1977, *W. B. Schofield 64411* (H), 2 Jul. 1957, *H. Persson s.n.* (H), Louise Island, 131°45′ W, 52°58′ N, 31 Jul. 1968, *W. B. Schofield 37346* (H), Mountain Creek, 23 Jun. 2002, *119983* (DUKE); Skeena River, 15 Jun. 1963, *W. B. Schofield 21650* (UBC); Vancouver Island, Fair Harbour, 5 Aug. 1984, *W. B. Schofield 82391* (UBC), Holberg, May 1937, *E. C. MacKenzie 400* (MICH), Port Renfrew, 4 May 1961, *W. B. Schofield 13732* (UBC), Ucluelet, 11 May 1909, *J. Macoun s.n.* (MICH).

U.S.A. Alaska: Evans Island, 1948, *W. J. Eyordam 5024* (MICH), *5045* (MICH); Juneau, 7 Aug. 1967, *F. J. Hermann 22027* (H); Kenai Peninsula, 149°26′27.1″ W, 60°4′ N, 2 Sep. 2006, *W. B. Schofield 125401* (UBC); Ketchikan, 15 May 1968, *I. A. Worley & G. Hamilton 6551* (H, MICH); Knight Island, 15 Oct. 1940, *W. J. Eyerdam s.n.* (MICH); Kuiu Island, 20 Aug. 1947, *W. J. Eyerdam 944* (MICH539681, MICH539685); Sitka, 135°22′ W, 57°7′ N, 16 May 2004, *W. B. Schofield 122835A* (UBC), Indian River Trail, 4 Aug. 1967, *Z. Iwatsuki, A. J. & E. Sharp 2424* (H); Whittier, 148°39′ W, 60°46′ N, 5 Jun. 2001, *W. B. Schofield 117656* (UBC); Yakobi Island, 14 Jun. 1957, *H. T. Shacklette 3904* (MICH); Yakutat, 2 Jun. 1946, *H. S. Mazaika 5102* (MICH), *5125* (MICH), *5126* (MICH), *5127* (MICH), *5128* (MICH), *5129* (MICH), *5130* (MICH), *5131* (MICH), *5132* (MICH), *5133* (MICH), *5134* (MICH), *5135* (MICH), *5136* (MICH), 19 Jul. 1945, *L. D. Stair 4871* (MICH), 18 Jul. 1945, *4872* (MICH), 19 Jul. 1945, *4872A* (MICH), *4880* (MICH), *5036* (MICH). Washington: Cascade Mountains, 24 Jul. 1898,

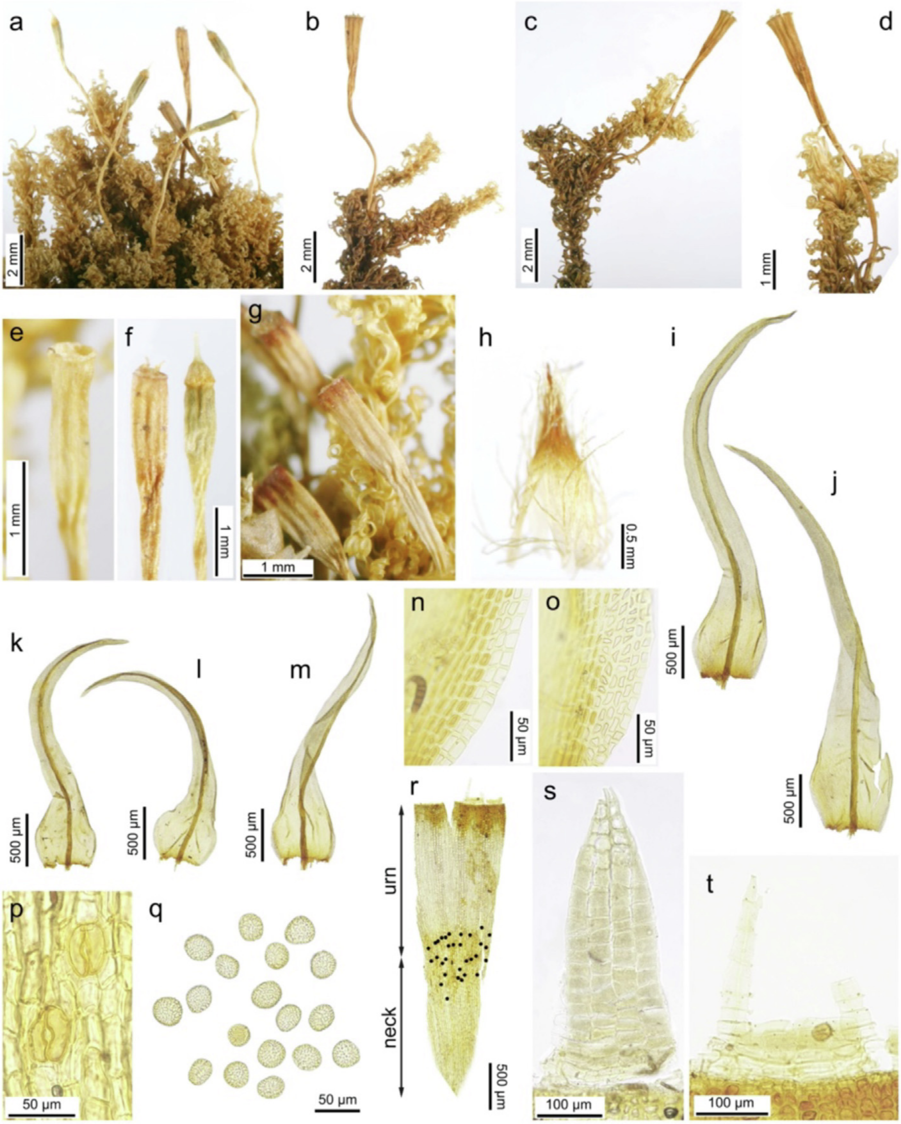


FIG. 130 – *Ulota obtusiuscula* Müll. Hal. & Kindb. a–d. Habit. e–g. Capsules in dry. h. Calyptra. i–j. Perichaetial leaves. k–m. Leaves. n–o. Marginal cells at leaf base. p. Stomata. q. Spores. r. Exothecial wall, with dots indicating stoma position. s. Exostome teeth. t. Endostome segments. (All from the isosyntype in FH except q from *D. H. Vitt & D. G. Horton* [non-type, FI]).

J. A. Allen 86 (MICH), *s.n.* (H); Clallam Co., 2 Jun. 2000, *D. H. Norris 98913* (UC), 17 May 2000, *98616* (UC); Jefferson Co., Olympic National Park, 19 May 1977, *D. H. Vitt s.n.* (H, HBG, MICH), 17 Aug. 1954, *G. W. Sharpe 117* (MICH), 20 Oct.

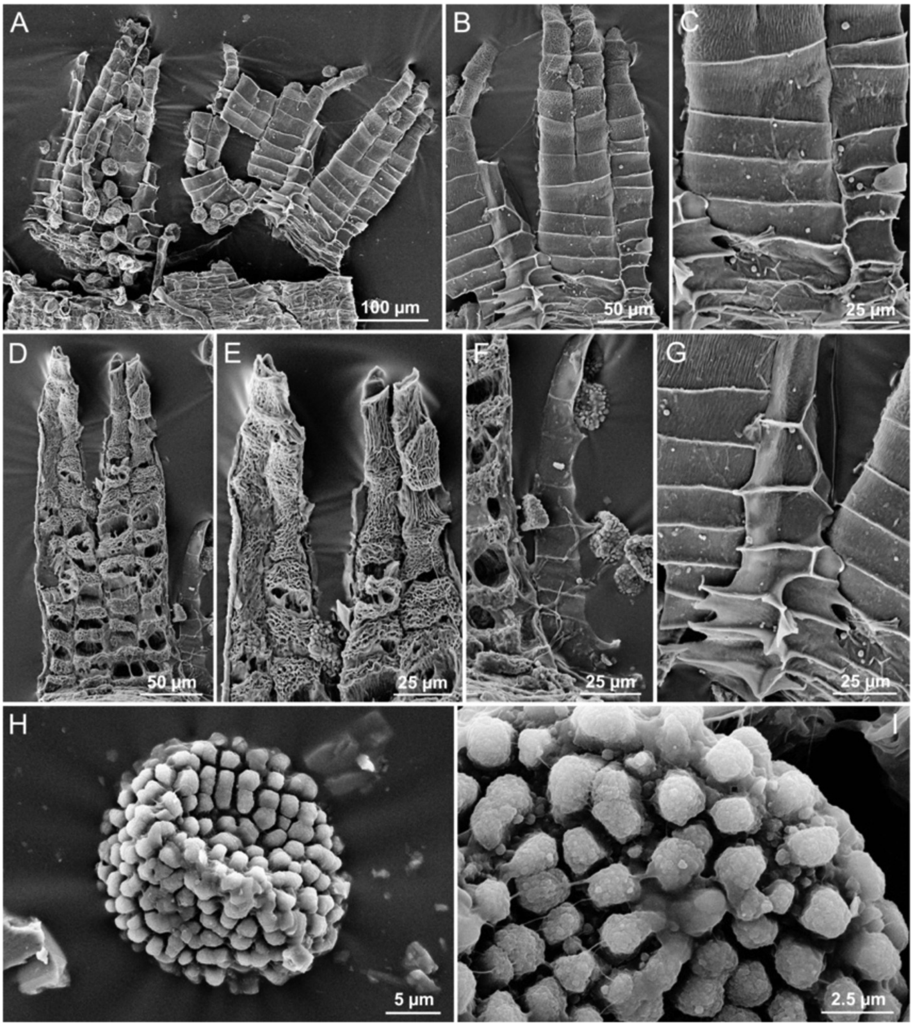


Fig. 131 – *Ulota obtusiuscula* Müll. Hal. & Kindb. A, inner view of peristome; B, inner surface of peristome; C, inner surface of basal exostome; D, outer view of exostome; E, outer surface of upper and middle exostome; F, outer surface of endostome; G, inner surface of basal endostome; H, a spore; I, surface ornamentation of a spore. (All from *Vitt & Horton* [non-type, FI]).

1954, *345* (MICH), 17 Aug. 1954, *E. Lawton 2488* (H3150934–35), 11 Jul. 1950, *A. J. Andrews 103* (MICH), 7 Jul. 1950, *A. L. Andrews 105* (MICH), 124°17′ W, 47°51′ N, 25 May 2000, *D. H. Norris 98852* (UC), 16 May 2000, *98494* (UC); Snohomish Co., 28 Feb. 1948, *W. J. Eyerdam 3004* (MICH), *3015* (MICH), 3 Dec. 1947, *E. J. Larrison s.n.* (MICH), 2 Jul. 1963, *F. J. Hermann 18527* (MICH).

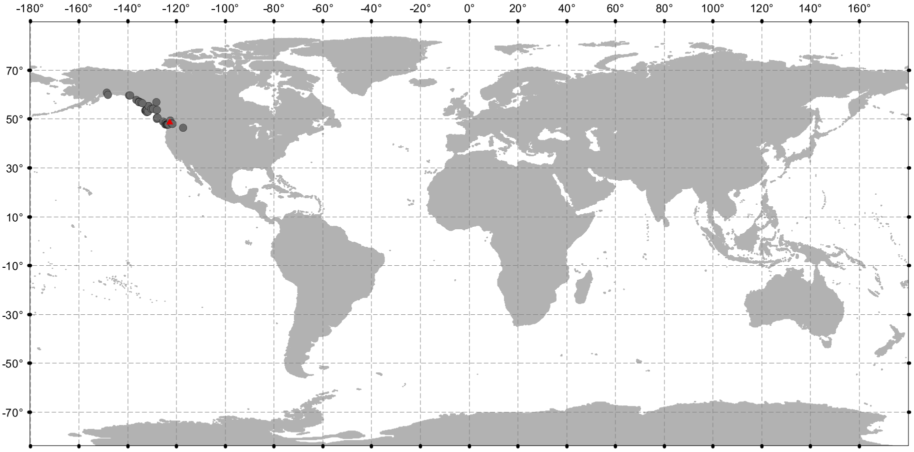


FIG. 132 – Distribution of *Ulota obtusiuscula* worldwide. The red triangle indicates the type locality.

35. **ULOTA PANCHENGIANA** Q.H. Wang & Y. Jia, Cryptog., Bryol. 39(4): 468, 1–28. TYPE: CHINA. Sichuan, Wenchuan Co., Weizhouzhen, Qipangoucun, Mt. Guangguangshan, 31°24′13″ N, 103°35′55″ E, 2400 m, on tree trunk, 27 Aug. 2002, *Y. Jia 06671b* (holotype, PE! isotype, MO!).

Plants 0.7–3 cm tall, yellowish green to olive-green above, brown to black below. Stems usually branched. Leaves strongly, rarely slightly crisped when dry, erect-patent to patent when moist, (1.6–) 2.2–3.7 (–4.3) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex long acuminate; leaf margin weak and irregularly recurved on one or both sides; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, (5–) 7–9 (–11) × (6–) 8–9 (–12) μm, thick-walled, often with two low simple papillae per cell, rarely branched; basal inner cells linear, rectangular, elongate-rectangular to vermicular, (8–) 14–20 (–44) × (3–) 5–6 (–11) μm, with thick wall, smooth; basal marginal cells differentiated in (1–) 3–5 (–7) rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves are somewhat longer, 4.1–5.2 mm. Vaginula is strongly hairy. Seta (1.5–) 3–6.5 (–8) mm long, twisted anticlockwise when dry. Capsule long exserted. Urn cylindrical to long-cylindrical, (1.1–) 1.4–1.7 (–2.3) mm long, slightly to strongly constricted below the mouth when dry and empty, mouth somewhat puckered, eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial throughout the urn. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, sometimes lying on the exothecium, lanceolate, densely and finely papillose outside, papillose or striate-papillose inside. Endostome segments 8, rarely with eight additional intermediate, shorter processes, principal segments linear-lanceolate, ≥2/3 length of teeth, uniseriate upper, irregularly biseriate at the base, 1/2–1/4 width of teeth, hyaline, smooth outside, finely papillose or slightly scabrous inside. Opercula not seen. Calyptra mitrate, naked. Spores spherical, finely papillose, (17–) 23–33 (–46) μm in diameter.

Illustration: Wang and Jia (2018b); figures 133 and 134.

Habitat: It is epiphytic on tree trunks and branches, such as *Populus*. There are some records of altitude: (1000–) 1800–2400 (–2569) m. It's occasionally mixed with *Orthotrichum schofieldii* and *O. erubescens*.

Distribution: It is **endemic** to Southwest China. Figure 135.

Notes: Compared with other Chinese congeners, *Ulota panchengiana* is a unique species due to its stomata distribution on the capsules. To date, only two species have stomata present at the central and upper part of the urn in the Northern Hemisphere, *i.e. U. panchengiana* and *U. rhytiore* (B.H. Allen) F. Lara, Garilleti, Albertos & Mazimpaka. However, *Ulota rhytiore* is easily distinguished from *U. panchengiana* by the emergent elliptical capsules, absent peristome, and densely hairy calyptra.

Additionally, there are only two species in the genus *Ulota* having calyptra always naked, *i.e. U. macrocalycina* from South America and *U. panchengiana*. Both have constricted cylindrical capsules, eight narrow endostome segments, urn-located stomata, and consistently naked calyptra. But *Ulota macrocalycina* differs in erect leaves, with more rows (4–10) of hyaline cells with thin walls at basal leaf margins, short seta (2–2.5 mm), and capsules without a puckered mouth. In the Southern Hemisphere, *Ulota panchengiana* also resembles *U. cochleata* from Australia in strongly crisped leaves, long exserted cylindrical capsules, eight narrow endostome segments, and urn-located stomata. *Ulota cochleata*, however, is different in the capsules, hardly constricted when dry, often fragile filiform endostome segments and densely hairy calyptra.

In China, *Ulota panchengiana* resembles *U. latisegmenta*, both having strongly crisped leaves and long exserted cylindrical capsules, but *U. latisegmenta* is distinguished by capsules never puckered at the mouth when dry, stomata restricted to the base of urn or transition zone between urn and neck, broad endostome segments and densely hairy calyptra.

No noteworthy variation within *Ulota panchengiana* was seen.

Key to *Ulota panchengiana* and its closely related species.

1. Capsules emergent, elliptical; Peristome absent................................*U. rhytiore*
1. Capsules long exserted, cylindrical; Peristome present....................................2
2. Leaves erect-appressed and sometimes sinuose when dry; leaf apex acute; hyaline cells at basal leaf margins with thin walls..........................*U. macrocalycina*
2. Leaves strongly crisped when dry; leaf apex long acuminate; hyaline cells at basal leaf margins with only thinckened transverse wall..................................3

3. Stomata confined to the base of urn or the transition zone between urn and neck; endostome segments 16, wide, lanceolate.......................... *U. latisegmenta*
3. Stomata on the urn, usually central and upper part; endostome segments eight, narrow, filiform to linear-lanceolate..4
4. Calyptra densely hairy; endostome segments filiform to linear, often fragile; capsules hardly constricted when dry... *U. cochleata*
4. Calyptra naked; endostome segments linear-lanceolate, never fragile; capsules variable constricted when dry, often somewhat puckered at mouth... *U. panchengiana*

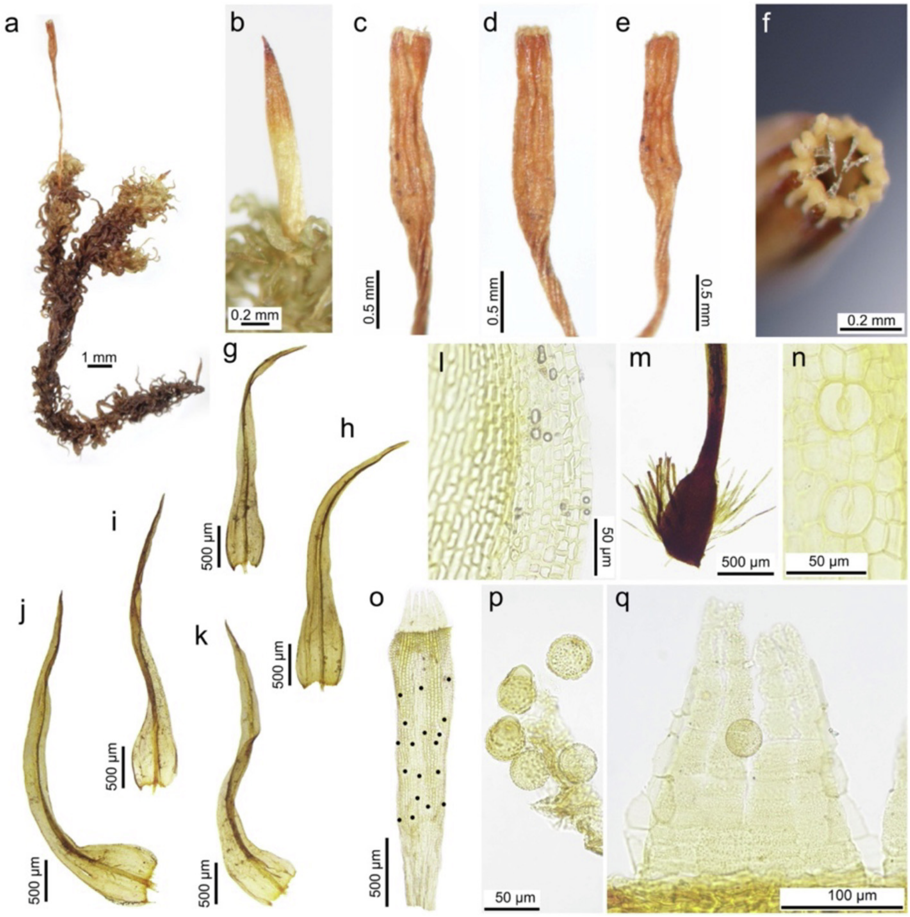


Fig. 133 – *Ulota panchengiana* Q.H. Wang & Y. Jia. a. Habit. b. Calyptra. c–e. Capsules in dry and empty. f. Capsule mouth viewed from above. g–i. Leaves. j–k. Perichaetial leaves. l. Marginal cells at leaf base. m. Vaginula. n. Stomata. o. Exothecial wall, with dots indicating stoma position. p. Spores. q. Peristome. (All from the holotype in PE and the isotype in MO except q from *M.-Z. Wang 50242a* [non-type, PE]).

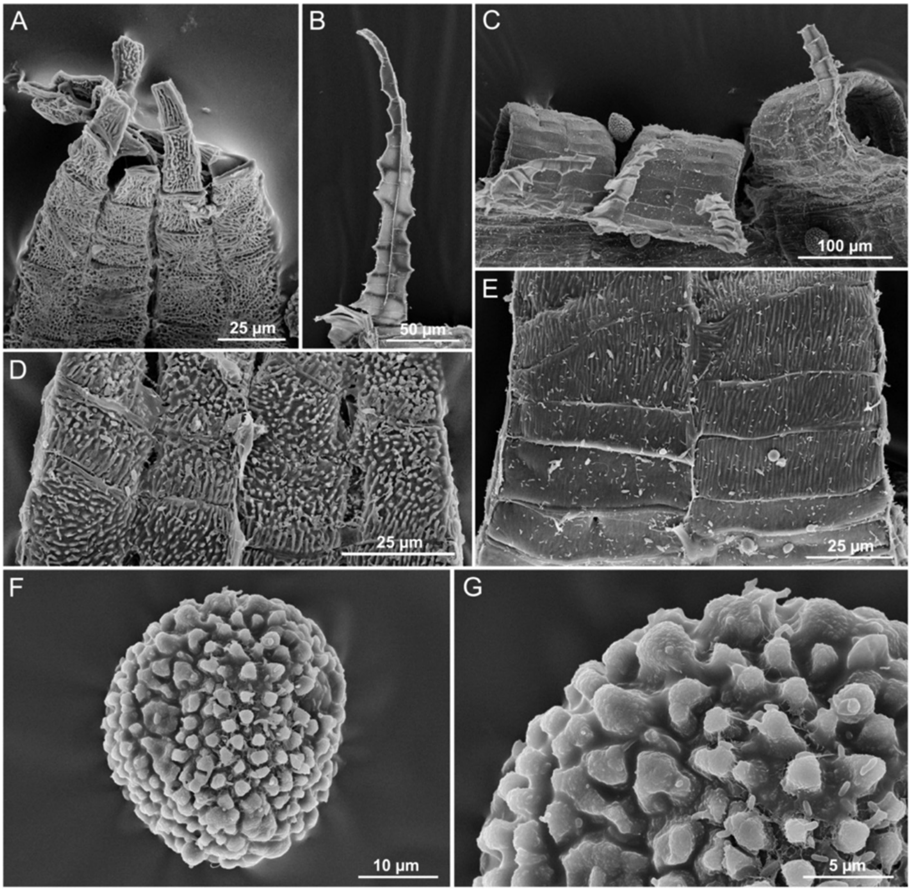


Fig. 134 – *Ulota panchengiana* Q.H. Wang & Y. Jia. A, outer view of exostome; B, outer surface of endostome; C, inner view of peristome; D, inner surface of upper exostome; E, inner surface of basal exostome; F, a spore; G, surface ornamentation of a spore. (All from *Jia 08188* [non-type, PE]).

Additional specimens studied (all in PE unless otherwise noted): **China**. Gansu: Wen Co., Qiujiaba, 25 Jun. 2006, *M.-Z. Wang 63009e*, 20 May 2007, *Y. Jia 09278b*, *09288*, 22 May 2007, *09326(3)*. Sichuan: Dujiangyan, longchi, 13 Jul. 1993, *M.-Z. Wang 49928*, 14 Jul. 1993, *M.-Z. Wang 50242a-1*, *P.-C. Wu 25350*; Jiulong Co., Hongba, 15 Apr. 2021, *Q.-H. Wang 2545d*; Kangding, Gonggashan National Nature Reserve, 7 Apr. 2021, *Q. He & Z.-Q. Yi 149*; Luding Co., Gonggashan National Nature Reserve, 6 Apr. 2021, *Q.-H. Wang 2171-1*, *2174-2*, *2178-1*, Hailuogou National Glacier Forest Park, 15 Apr. 2021, *Q.-H. Wang* 2556, 18 Apr. 2021, *Q.-H. Wang 2677*, 2678-1, Hailuogou Ganheba, 10 Oct. 2021, *Z.-Q. Yi Q291*, *Q292c*, Yanzigou, 18 Apr. 2021, *Y. Jia & L. Luo 20572-2*, 12 Oct. 2021, *Z.-Q. Yi Q499*, Yajiageng, 18 Apr. 2021, *Q. He & Z.-Q. Yi 838-1*; Mianning Co., Yele, 28°56.283″ N,

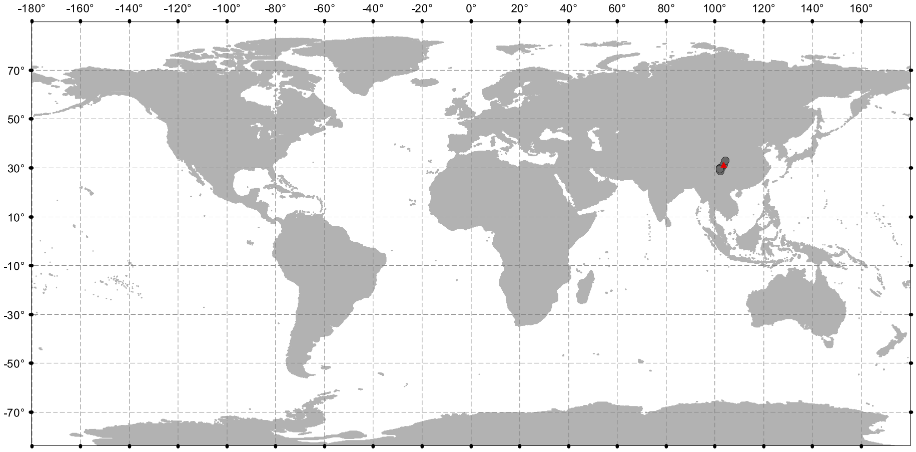


FIG. 135 – Distribution of *Ulota panchengiana* worldwide. The red triangle indicates the type locality.

102°06.268″ E, 9 Jul. 2005, *Y. Jia 08188*; Shimian Co., Gonggashan National Nature Reserve, 7 Apr. 2021, *Q.-H. Wang 2222-2*, *2237-2*, *2253-4*, *2256*, *2257*, *2265*, *2278-2*, *2280*, 8 Apr. 2021, *Q.-H. Wang 2284-2*, *2286*; Tianquan Co., 6 May 1977, *Q. Li 983* (IFP), 7 May 1977, *Q. Li 1005* (KUN), Labahe Nature Reserve, 30°10′55″–11′37″ N, 102°25′03″–25′48″ E, 27 Jun. 2015, *N. R. Gaowa Z650*; Wenchuan Co., Qipangoucun, 31°24′13″ N, 103°35′55″ E, 22 Aug. 2002, *Y. Jia 06817*, 27 Aug. 2002, *06666c*, *06671-b*.

36. **ULOTA PERBREVISETA** Dixon & Sakurai, Bot. Mag. 49: 139. 1935. ≡ *Ulota japonica* var. *perbreviseta* (Dixon & Sakurai) W.S. Hong & Ando, Theses Catholic Med. Coll., Seoul 3: 380. 1959. *invalid, basionym not cited.* TYPE: JAPAN. Hondo, “Prov. Ohmi, Mt. Ibuki, an Sträuchern, (Coll. K. Sakurai Typus-Nr. 1070 auch bei Dixon Mai-1923” (holotype, BM000852410!).

Plants ca. 1.5 cm tall, yellow on the top, gradually dark below. Stems usually branched. Leaves moderately to strongly crisped when dry, wide-spreading when moist, (1.7–) 2.2–2.7 (–3.2) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex long acuminate; leaf margin plane, rarely partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, oblong, (5–) 7–10 (–14) × (6–) 8–10 (–12) μm, thick-walled, with low papillae; basal inner cells linear, rhombic, rectangular, (11–) 25–39 (–58) × (2–) 3–6 (–9) μm, with thick wall, smooth; basal marginal cells often differentiated in 4–6 rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves somewhat longer, (2.3–) 2.4–3.2 (–3.4) mm. Vaginula naked. Seta (0.5–) 0.6–1.2 (–1.3) mm long, sometimes twisted anticlockwise when dry. Capsule fully emergent, 1.5–1.8 mm long. Urn short-cylindrical when empty and dry, subglobose when moist, hardly constricted below the mouth when empty and dry, eight furrows along the entire length, with prominent ribs alternately. Neck short, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, four to five cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between the urn and neck or the central part of capsules. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8

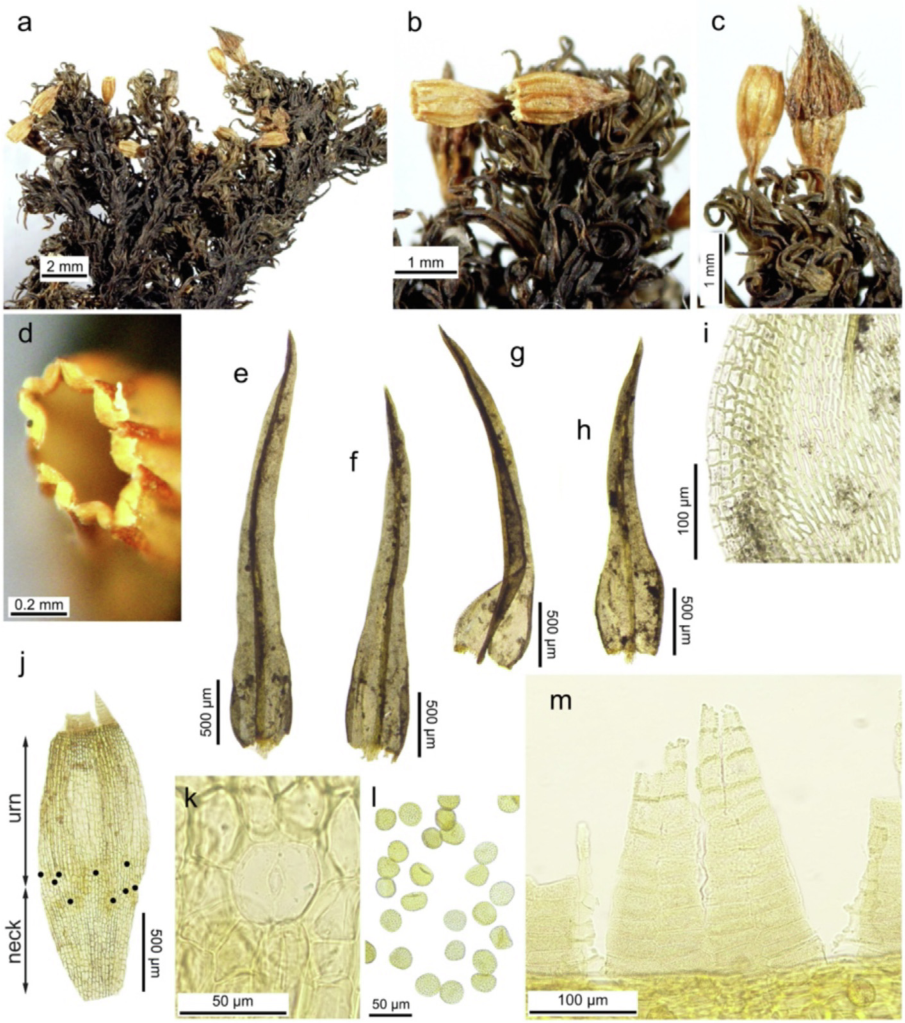


FIG. 136 – *Ulota perbreviseta* Dixon & Sakurai. a. Habit. b. Capsules in dry and empty. c. Calyptra. d. Capsule mouth viewed from above, with endostome segments caducous. e–h. Leaves. i. Marginal cells at leaf base. j. Exothecial wall, with dots indicating stoma position. k. Stoma. l. Spores. m. Peristome. (All from the holotype in BM).

pairs, recurved when dry, sometimes lying on the exothecium, lanceolate, densely and finely papillose on both sides. Endostome segments 8, narrow-lanceolate, almost as long as teeth, uniseriate or partially biseriate, hyaline or pale yellow, smooth outside, finely papillose inside. Opercula yellowish, usually with a short beak. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (26–) 28–31 (–34) μm in diameter.

Illustration: Noguchi and Iwatsuki (1989), Guo *et al.* (2010) and Wang and Jia (2012a); figures 136 and 137.

Habitat: It grows on trunks and branches of trees, such as *Deutzia nakaiana*. There are only two altitude records, ranging from 1400 to 1500 m.

Distribution: It occurs in China, Japan, and South Korea. Figure 138.

Notes: *Ulota perbreviseta* is a rare species and easily distinguished by its very short seta, and short-cylindrical capsules hardly constricted when dry.

Ulota perbreviseta was treated by Hong and Ando (1959) as a variety of *U. japonica*. We do not know their reasons because the paper is not available to us. But according to our study, *Ulota japonica* differs from *U. perbreviseta* in the often flexuose leaves, more rows of hyaline cells at basal leaf margins (7–10 rows), exserted capsules that strongly constricted when dry, sparsely hairy to naked calyptra and small spores (19–22 μm). In *Ulota*, there are four species with emergent capsules, besides *U. perbreviseta*, including *U. barclayi* from North America, *U. gymnostoma* from China, and *U. rhytiore* from tropical America. However, *Ulota gymnostoma* and *U. rhytiore* differ from *U. perbreviseta* in the elliptical capsules with the puckered mouth when dry and absent peristome, while *U. barclayi* differs in the smaller leaves (1.6–1.8 mm) that erect-appressed to flexuose when dry, leaf basal marginal cells with thin walls, strongly constricted capsules, sparsely hairy calyptra and smaller spores (19–25 μm).

No noteworthy variation within *Ulota perbreviseta* was seen.

Key to *Ulota perbreviseta* and its closely related species.

1. Capsules fusiform, oblong-cylindrical or elliptical, with puckered mouth when dry; peristome absent........2
1. Capsules cylindrical to short-cylindrical, mouth never puckered when dry; peristome double........3
2. Capsules fully emergent to short exserted; stomata restricted to the base of urn or the junction of urn and neck; leaves strongly crisped when dry........*U. gymnostoma*
2. Capsules emergent; stomata scattered throughout the urn; leaves strongly flexuose to spiral when dry........*U. rhytiore*
3. Leaves smaller (1.6–1.8 mm), erect-appressed to flexuose when dry; leaf basal marginal cells with thin walls; perichaetial leaves distinctly differentiated........*U. barclayi*
3. Leaves relatively large (1.7–2.7 mm), flexuose to strongly crisped when dry; leaf basal marginal cells with thickened transverse walls; perichaetial leaves hardly differentiated........4

4. Leaves often flexuose when dry; hyaline cells at basal leaf margins in more rows (7–10 rows); capsules exserted, strongly constricted when dry; calyptra sparsely hairy or naked; spores small, 19–22 μm..*U. japonica*
4. Leaves strongly crisped when dry; hyaline cells at basal leaf margins in less rows (4–6 rows); capsules emergent, hardly constricted when dry; calyptra densely hairy; spores large, 28–31 μm...*U. perbreviseta*

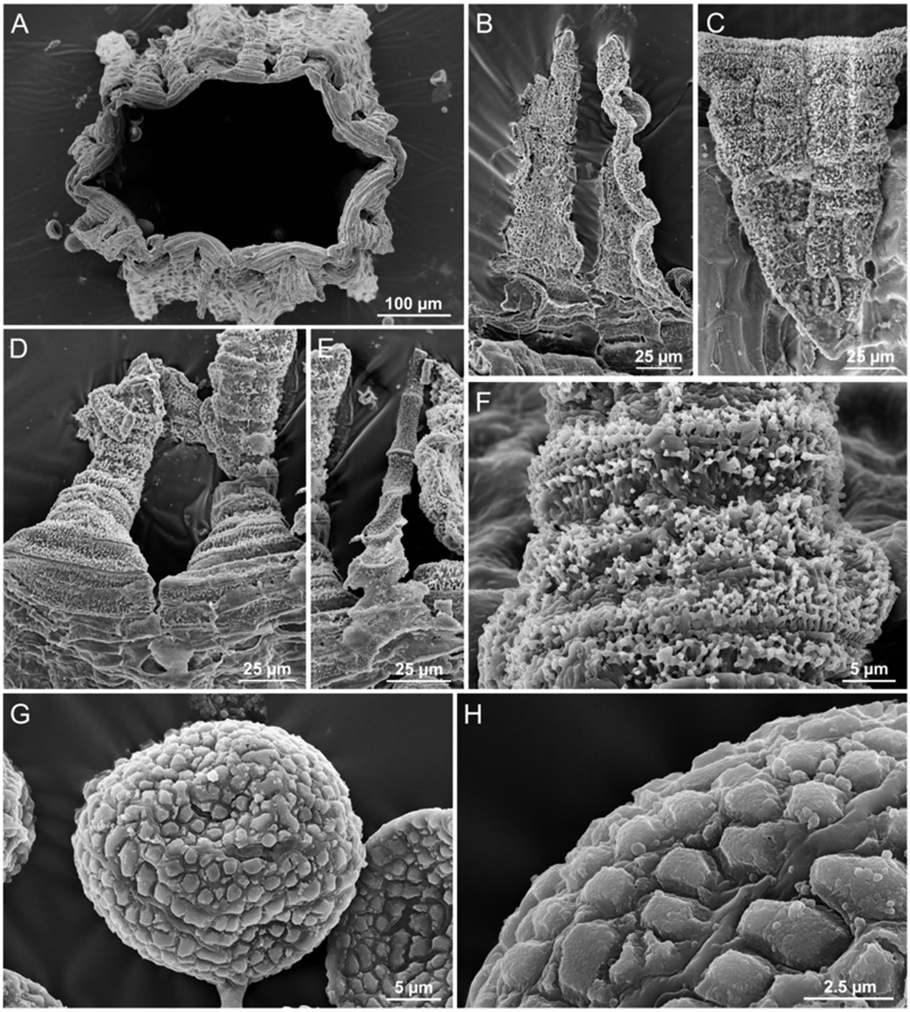


FIG. 137 – *Ulota perbreviseta* Dixon & Sakurai. A, overview of peristome; B, outer view of exostome; C, inner surface of upper exostome; D, inner surface of basal exostome; E, inner surface of endostome; F, inner surface of middle exostome; G, spores; H, surface ornamentation of a spore. (All from *Toyama 3186* [non-type, KYO]).

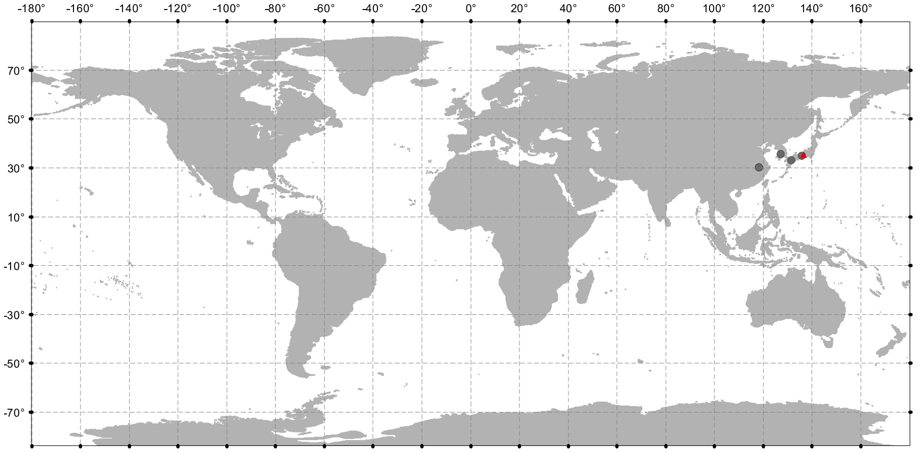


FIG. 138 – Distribution of *Ulota perbreviseta* worldwide. The red triangle indicates the type locality.

Additional Specimens Examined: **China**. ANHUI: Huangshan, 25 Apr. 1957, *P.-C. Chen et al. 6801b* (PE), 27 Apr. 1957, *7047c* (PE), 23 Aug. 1962, *X.-L. Chen 615-2* (IFP).

Japan. KYOTO: Mt Kuriyama, 29 Mar. 1938, *s.coll. 2651* (KYO); OITA: summit of Mt. Yufu, 14 Oct. 1954, *A. Noguchi 34169* (S).

South Korea. JEOLLABUK-DO: Mt. Deogyu, 12 Aug. 1938, *R. Toyama 3186* (KYO).

37. **ULOTA PERICHAETIALIS** (Sainsbury) Goffinet, Bryol. Twenty-first Cent. 153. 1998. ≡ *Bryodixonia perichaetialis* Sainsbury, Trans. & Proc. Roy. Soc. New Zealand 75: 177. 36 f. 1. 1945. TYPE: NEW ZEALAND. North Island, Taranaki, Mt. Egmont, Fantham's Peak Track, on bark of subalpine scrub, alt. 1219 m, 16 Jan. 1945, *G. O. K. Sainsbury 6476* (lectotype, WELT-M005689! designated by Fife, 2017).

Plants 1–3.5 cm tall, yellow to green above, brown to black below. Stems usually branched. Leaves strongly crisped when dry, erect-patent to patent when moist, (2.3–) 2.9–3.3 (–3.8) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex long acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, oblong, (6–) 7–12 (–17) × (6–) 7–9 (–13) μm, thick-walled, with low papillae; basal inner cells linear, rectangular, elongate-rectangular to vermicular, (20–) 26–37 (–49) × (1–) 2 (–3) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in (1–) 3–5 (–7) rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves are remarkably longer, (3.8–) 4–4.6 (–5.4) mm. Vaginula not seen. Seta is very short, ca. 0.5 mm. Capsule immersed, 1.4–1.7 mm long. Urn cylindrical, moderately constricted below the mouth when dry and empty, with eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, four to five cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between urn and neck. Preperistome not seen. Peristome single. Exostome teeth 16, often united into 8 pairs, recurved when dry, often lying on the exothecium, lanceolate, densely papillose outside, striate inside. Endostome segments are absent. Opercula with a short to medium long beak. Calyptra mitrate, small, sparsely to moderately hairy. Spores spherical, finely papillose, (34–) 40–45 (–50) μm in diameter.

Illustration: Figures 139 and 140.

Habitat: It grows on trunks and branches of trees, such as *Coprosma*, *Dracophyllum*, *Nothofagus,* and *Olearia*. There are only three altitudinal records, from 840 to 1326 m. It is occasionally mixed with *U. crispa*.

Distribution: It is **endemic** to New Zealand. Figure 141.

Notes: *Ulota perichaetialis* is a quite unique species in the genus, characteristic of remarkably longer perichaetial leaves, immersed capsules, and quite a small calyptra. Although its morphology seems such different from other *Ulota* species, molecular evidence suggests that it belongs to the genus (Goffinet and Vitt, 1998).

In *Ulota*, all species have, if not always, exserted capsules, except *U. rhytiore* from central America, *U. perbreviseta* from Japan, and *U. perichaetialis*, in which the former two have emergent capsules. Besides that, *U. rhytiore* is easily distinguished by the elliptical capsules with the puckered mouth when dry, absent peristome, and urn-located stomata, while *U. perbreviseta* differs in short-cylindrical capsules that hardly constricted when dry and double peristome.

In addition, perichaetial leaves in *Ulota* are generally longer than vegetative leaves, but only the ones in *U. perichaetialis* are the most. *Ulota germana* also has much longer perichaetial leaves, and it is an important diagnostic character. However, *Ulota germana* differs from *U. perichaetialis* in more rows (6–10) of hyaline cells at basal leaf margins, exserted capsules, well-developed endostome segments, and smaller plants (0.5–2 cm).

No noteworthy variation within *Ulota perichaetialis* was seen.

Key to *Ulota perichaetialis* and its closely related species.

1. Capsules fusiform, oblong-cylindrical or elliptical with puckered mouth when dry; peristome absent; stomata throughout on the urn...................... *U. rhytiore*
1. Capsules short-cylindrical to cylindrical without puckered mouth; peristome present, single or double; stomata on the lower part of urn or at the junction between urn and neck...2
2. Capsules immersed; peristome single; perichaetial leaves extremely longer; calyptra small; spores large, 40–45 μm................................... *U. perichaetialis*
2. Capsules emergent to exserted; peristome double; perichaetial leaves somewhat or much longer; calyptra large; spores small, 28–35 μm....................................3
3. Capsules short to long exserted, cylindrical, strongly constricted when dry; more rows of hyaline cells at basal leaf margins (6–10); perichaetial leaves much longer.. *U. germana*

3. Capsules fully emergent, short-cylindrical, hardly constricted when dry; less rows of hyaline cells at basal leaf margins (4–6); perichaetial leaves somewhat longer..*U. perbreviseta*

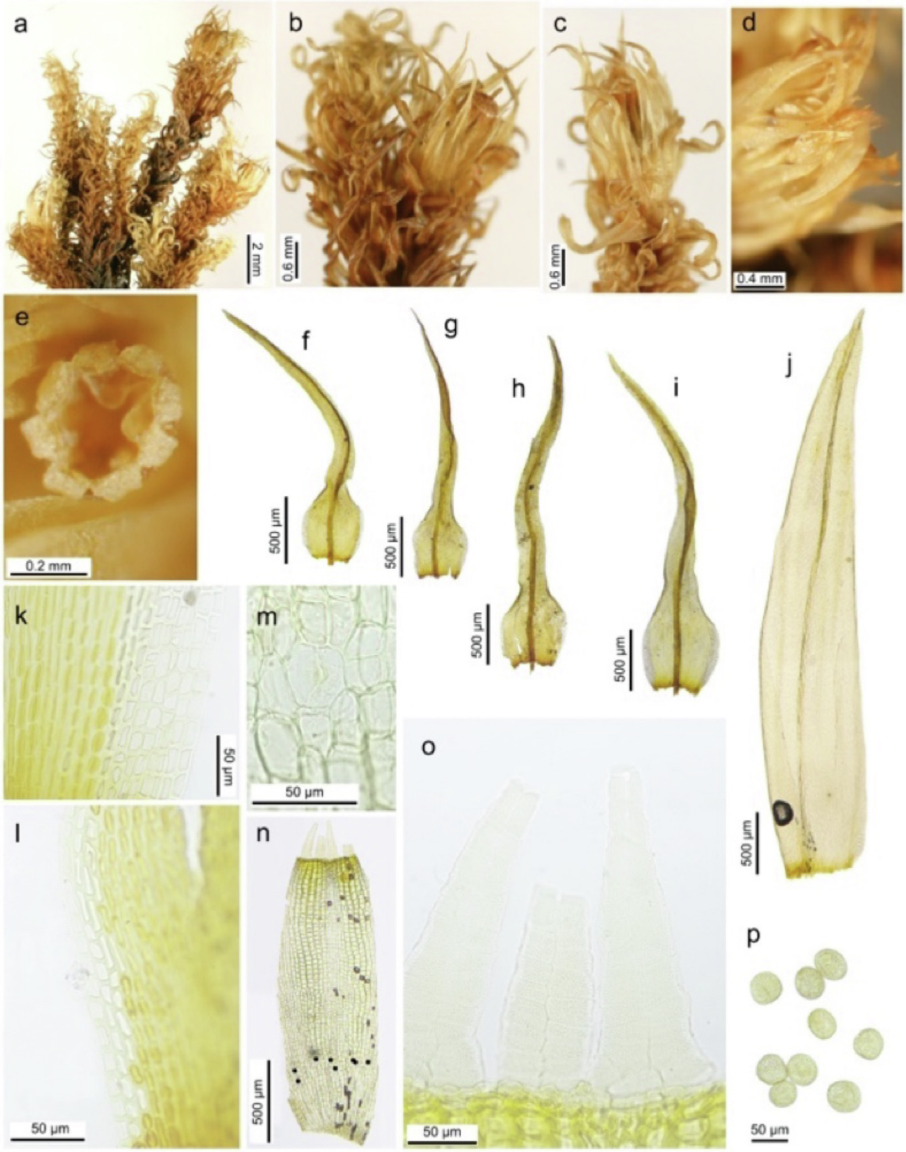


FIG. 139 – *Ulota perichaetialis* (Sainsbury) Goffinet. a. Habit. b–c. Immersed capsules in dry. d. Calyptra. e. Capsule mouth viewed from above. f–i. Leaves. j. Perichaetial leaves. k–l. Marginal cells at leaf base. m. Stoma. n. Exothecial wall, with dots indicating stoma position. o. Peristome. p. Spores. (All from the lectotype in WELT).

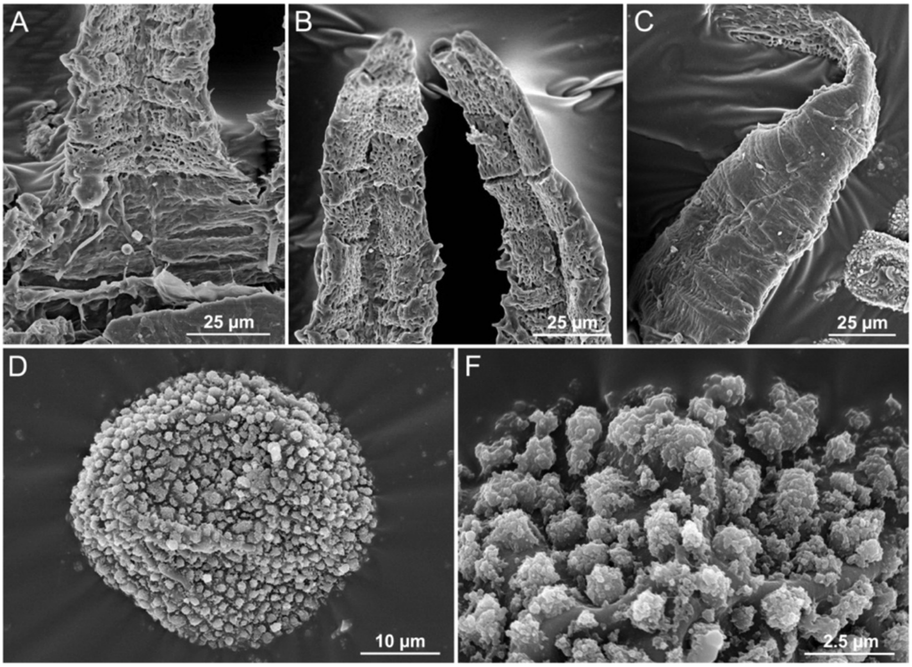


FIG. 140 – *Ulota perichaetialis* (Sainsbury) Goffinet. A, outer surface of basal exostome; B, outer surface of upper exostome; C, inner surface of exostome; D, a spore; F, surface ornamentation of a spore. (All from the lectotype in WELT).

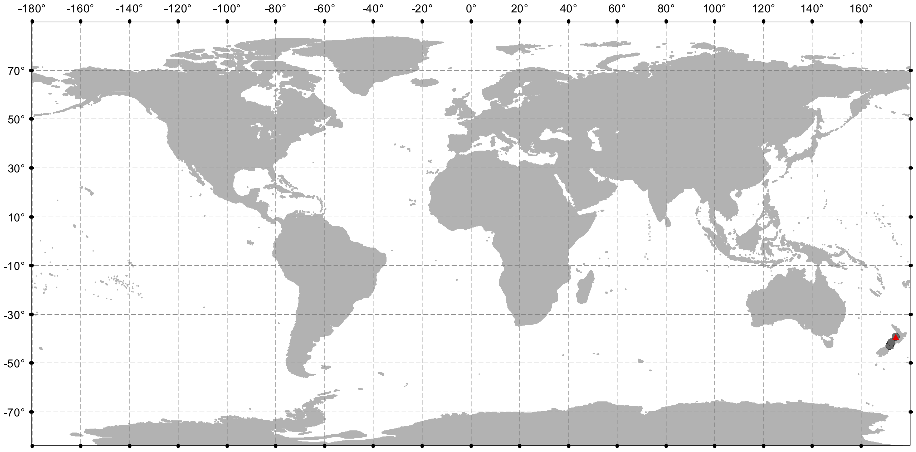


FIG. 141 – Distribution of *Ulota perichaetialis* worldwide. The red triangle indicates the type locality.

Additional Specimens Examined: **New Zealand**. CANTERBURY: Arthurs Pass National Park, Pegleg Creek, 171°33′ E, 42°54′ S, 1 Feb. 1986, *A. J. Fife 7409* (CHR), 1 Feb. 1986, *C. D. Meurk s.n.* (CHR); upper Hawdon River, Cass-Canterbury, 31 Jan. 1973, *L. Visch 2617* (CHR). NELSON: Scarlett Range, Shelter Rock Basin, 9 Feb. 1987, *A. J. Fife 8083* (CHR). TARANAKI: Monganui Hut on Mt Egmont, Jan. 1955, *E. A. Hodgson s.n.* (CHR). WEST COAST: Grey Co., Paparoa Mountains, 12 Apr. 1983, *A. J. Fife 5452* (CHR).

38. **ULOTA PHYLLANTHA** Brid., Muscol. Recent. Suppl. 4: 113. 1819[1818]. ≡ *Orthotrichum phyllanthum* (Brid.) Steud., Nomenclator Botanicus 2: 304. 1824. ≡ *Weissia phyllantha* (Brid.) Lindb., Musci Scandinavici 28. 1879. TYPE: DENMARK. “E Danice maritimus. Ludwigius. 1811” (holotype, B31024101!).

Orthotrichum fasciculare Brid., Bryologia Universa 1: 790. 1827. TYPE: CANADA. Terre Neuve, *LaPylaie*, 1825 (holotype, B).

Orthotrichum jutlandicum Brid., Bryologia Universa 1: 296. 1826. *illegitimate, type of earlier name included.*

Orthotrichum maritimum (Müll. Hal. & Kindb.) Kindb., European and N. American Bryineae (Mosses) 2: 308. 1897. ≡ *Ulota maritima* Müll. Hal. & Kindb., Catalogue of Canadian Plants, Part VI, Musci 84. 1892. ≡ *Weissia maritima* (Müll. Hal. & Kindb.) E. Britton, Bulletin of the Torrey Botanical Club 21: 72. 1894. TYPE: MIQUELON ISLAND. *Delamare* (syntypes, PC! S!); CANADA. British Columbia, Hastings, 11 Apr. 1889, *Macoun* (syntype, NY); U.S.A. Alaska, Unalaska Island, and Kodiak Island, 22 Sep. 1891, *Macoun* (syntypes, CANM, S!).

Ulota jutlandica I. Hagen, Det K. Norske Videnskabers Selskabs Skrifter 1907 (13): 29. 1908. *invalid, cited as synonym.*

Ulota scotica Stirt., Annals of Scottish Natural History 14(54): 106. 1905.

Ulotrichum phyllanthum Schimp., Bryologia Europaea 3: 1 (fasc. 46–47 Consp. vol 3: I). 1851. *invalid combination.*

Plants 1–3.5 cm tall, green above, gradually brown below. Stems usually branched. Leaves strongly crisped when dry, patent to spreading when moist, (2.5–) 2.7–3.7 (–3.9) mm long; leaf lamina narrow lanceolate, unistratose; leaf base slightly wide, ovate, distinctly concave; apex long acuminate; leaf margin plane and partially recurved; costa strong, ending shortly below the apex, sometimes protruding after gemmae fallen. Upper and middle laminal cells oblong, sometimes rounded, (7–) 11–16 (–22) × (3–) 4–7 (–10) μm, thick-walled, with 2 low papillae per cell; basal inner cells linear, rectangular, elongate-rectangular to vermicular, (19–) 37–64 (–94) × (1–) 2–4 (–6) μm, with strongly thickened wall, smooth; basal marginal cells not differentiated. Gemmae is cylindrical or club-shaped, red or orange, and usually abundant on the apex of leaves at the top of branches or stems.

Dioicous. Perichaetial leaves hardly differentiated, 3.1–3.4 mm. Vaginula naked. Seta ca. 5 mm long, twisted anticlockwise when dry. Capsule long exserted, ca.

1.4 mm long. Urn cylindrical to short-cylindrical, moderately constricted below the mouth when dry and empty, eight furrows almost along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, lying on the exothecium, lanceolate, densely and finely papillose on both sides. Endostome segments 16, often 8 caducous alternately, linear, ca. 2/3 length of teeth, uniseriate or partially biseriate, 1/4–1/5 width of teeth, hyaline, smooth outside, finely papillose inside. Opercula with a long beak, yellowish, usually with a reddish basal ring. Calyptra mitrate, moderately hairy. Spores spherical, finely papillose, (16–) 17–19 (–20) μm in diameter.

Illustration: Malta (1927), Nyholm (1960), Seppelt (1978), Smith (1978), Crum and Anderson (1981), Ireland (1982), Vitt (2014) and Wang and Jia (2016); figures 142 and 143.

Habitat: It is epiphytic on tree branches and trunks, such as alder, chestnut, *Fraxinus*, *Nothofagus*, *Picea* (spruce), *Populus*, *Pyrus*, *Salix*, and *Sambucus*. It also often grows on rocks. There are many records of altitude, ranging from sea level to 120 m, rarely up to 295 m. It sometimes grows mixed with *Ulota crispa* or *Orthotrichum sp.*

Distribution: It is common in seashores of the North Hemisphere except East Asia, rare in the southern part of the South Hemisphere. Wijk *et al.* (1969) indicated it is present in Africa, but no detailed information was provided, and we have not obtained any specimens from this area, therefore it is not considered in this study. Figure 144.

Notes: *Ulota phyllantha* is the most easily diagnosable taxa in the genus and one of two species (with *U. crispa*) distributed in both hemispheres. It usually produces abundant reddish gemmae at the tip of the leaves on the top of branches or stems, which is almost never present in any other species in the genus. The leaves in *Ulota phyllantha* are strongly crisped, and the basal marginal leaf cells are hardly differentiated. It is also the only dioicous species in *Ulota*.

Unlike other *Ulota spp.*, *U. phyllantha* rarely produces capsules, and we have only seen it three times during this study. Two of them are from U.K., respectively Northern Ireland (*W. N. Tetley s.n.*, BBSUK), and Scotland (*D. F. Chamberlain*, E). The former has only one capsule on which the teeth are lost; thus, we do not dissect it, while the latter is well preserved. The third specimen with capsules is from Canada, British Columbia (*W. B. Schofield 100736*, DUKE) and is also in good condition. Therefore, the description of sporophytic characters here is taken from the two specimens from Scotland and British Columbia. We found eight endostome segments in the Scotland collection and 16 in the British Columbia collection. But this inconsistency is probably because eight of the 16 endostome segments are easy to fall off alternately, so sometimes only eight are seen (see figure 143). It is probably also the case in the study of Crum and Anderson (1981). Nevertheless, in their description, the capsules are not or slightly constricted when dry, and the endostome segments are wider.

Recently, *Ulota phyllantha* was reported from Asia for the first time (Suzuki and Iwatsuki, 2011), but the two cited collections (*T. Suzuki 60759 & 60760*, NICH) from Japan are probably misidentified, although we have not seen them yet. Some sporophytic characters they described are obviously different from those of Scottish and Canadian materials, such as broadly oblong-ovoid capsules with a long neck, much shorter seta (1–2.7 mm), eight smooth endostome segments and larger spores (20–22 μm). Most importantly, the gemmae in Japanese materials are born on the adaxial surface of costa rather than the leaf apex, which is distinctly not consistent with *Ulota phyllantha*. Consequently, it should be excluded from the flora of Asia.

Gametophytically, *Ulota phyllantha* resembles *U. novo-guinensis* and *U. splendida* from Papua New Guinea. They all have strongly crisped leaves, ovate leaf bases, and hardly differentiated cells at basal leaf margins. Furthermore, *Ulota phyllantha* shares the larger plants with *U. splendida*, while sporophytically shares the 16 linear endostome segments with *U. novo-guinensis*. However, besides the absent gemmae, *Ulota splendida* is also readily separated by the slightly sparse arrangement of leaves on stems or branches, the common long-cylindrical capsules, the very long seta (7–8 mm), the eight endostome segments, and the large spores (29–33 μm), while *U. novo-guinensis* is easily distinguished by the smaller plants (0.7–1.7 cm), the smaller leaves (1.9–2.1 mm), the smooth endostome segments and the multicellular spores (110–125 μm).

Most recently, this species was erected as a new genus (Plášek *et al.*, 2015), *i.e.* *Plenogemma* Plášek, Sawicki & Ochyra, but we considered that this still needs more strong molecular evidence and thus view this taxon as a member of *Ulota* here.

The plant height of *Ulota phyllantha* was described as up to 5.5 cm previously (Vitt, 2014), but we have not seen it in this study. The Canadian materials with sporophytes (*W. B. Schofield 100736*, DUKE) have more acuminate leaves and shorter gemmae.

Key to *Ulota phyllantha* and its closely related species.

1. Plants small, 0.7–1.7 cm; leaf apex acuminate; leaves short, 1.9–2.1 mm; endostome teeth smooth; spores multicellular, 110–125 μm.. *U. novo-guinensis*
1. Plants large, 1–3.5 cm; leaf apex long acuminate; leaves quite long, 2.7–3.7 mm; endostome teeth slightly coarse or finely papillose; spores unicellular, 17–33 μm..2
2. Gemmae never seen; leaves arranged relatively sparsely on stems and branches; capsules usually seen, long-cylindrical; seta very long, 7–8 mm; endostome segments 8, narrow-lanceolate; spores large, 29–33 μm.................... *U. splendida*
2. Gemmae abundant at the tip of the leaves on the top of branches or stems; leaves arranged densely on stems and branches; capsules rarely seen, cylindrical to short-cylindrical; seta short, ca. 5 mm; endostome segments 16, linear; spores much smaller, 17–19 μm.. *U. phyllantha*

Additional Specimens Examined: **Argentina**. TIERRA DEL FUEGO: Bahia Lapataia, 10 Jan. 1970, *H. Roivainen s.n.* (H), *1908* (MICH), 12 Jan. 1970, *s.n.* (H); s. loc., 12 Dec. 1999, *D. H. Norris 97062* (H).

Australia. MACQUARIE ISLAND: s. loc., s. date, *N. R. Laird 284* (BM).

Canada. BRITISH COLUMBIA: Queen Charlotte Island, *W. B. Schofield 55898* (H), *100736* (DUKE); Sonora Island, 125°12′ W, 50°19′ N, *W. B. Schofield 642623* (H); Strait of Georgia, Mayne Island, 17 Jul. 1980, *R. Zander 4378* (MO); Vancouver, Brooks Peninsula, 127°50′ W, 50°10′ N, *W. B. Schofield 68620* (H), near Tofino Airport, *W. B. Schofield 26677-2* (UBC); Wells Islet, N.W. of Banks Island, 6 Jun. 1970, *W. B. Schofield 42040* (MICH). NEW BRUNSWICK: Charlotte Co., 66°31′ W, 45° 7′ N, 19 Jul. 1970, *R. R. Ireland 13360* (H). NEWFOUNDLAND: Avalon Peninsula, Little Chance Cove, 20 May 1975, *G. R. Brassard 10022* (H, MICH), mouth of Back River, 27 May 1975, *G. R. Brassard 10106* (H), Cape St. Mary's, 54°12′ W, 46°49′ N, 6 Jun. 1978, *G. R. Brassard 12057* (H, MICH), Bay Roberts East Shoreline Heritage Walk, 53°12′ W, 47°37′ N, 10 Sep. 2007, *R. A. Pursell 12815* (MO), *12816* (MO), Maritime Barrens Ecoregion, 53°12′ W, 47°37′ N, *B. Allen 28702* (MO); Biscay Bay, Ferryland, 53°17′ W, 46°44′ N, 7 Jun. 1949, *R. Tuomikoski 349* (H, MICH); Cow Head, St. Barbe, 57°54′ W, 49°52′ N, 10 Aug. 1949, *R. Tuomikoski 4994* (H, MICH); Maidstone, 16 Jul. 1968, *C. Williams 1620* (MICH); Western Brook, 19 Jul. 1974, *G. R. Brassard 9238* (H); White Bay North District, 55°54′ W, 50°54′ N, 2 Aug. 1976, *A. J. Fife 1708* (MICH), 55°30′ W, 51°36′ N, 16 Aug. 1976, *A. J. Fife 1935* (MICH), 55°28′ W, 51°32′ N, 18 Aug. 1976, *A. J. Fife 1968* (MICH), 55°38′ W, 51°20′ N, 19 Aug. 1976, *A. J. Fife 2016* (MICH), 55°44′ W, 51°34′ N, 22 Aug. 1976, *A. J. Fife 2082* (MICH). NOVA SCOTIA: Cape Breton Island, Richmond Co., 25 Jun. 1984, *D. H. Vitt 31263* (MICH); Point Michaud, Richmond Co., 31 Jul. 1981, *B. H. Allen 2337a* (MICH). QUEBEC: Grindstone Island, Magdalen Islands, 12 Aug. 1969, *R. Reilly 1724* (MICH); Iles-de-la-Madeleine, Ile Brion, 8 Aug. 1968, *J. L. De Sloover 8.467* (H, MICH).

Chile. LOS LAGOS: Cabo san Pablo, 26 Jan. 1929, *H. Roivainen s.n.* (H). MAGALLANES: Antartica Chilena, Comuna Cabo de Hornos, Islas Wollaston, 67°18′ 01″ W, 55°49′23″ S, 23 Jan. 2004, *B. Allen 26689* (MO), 67°13′27″ W, 55°57′46″ S, 24 Jan. 2004, *B. Allen 26713* (MO).

Denmark. FAROE ISLANDS: Föroyar, Streymoy, 19 Jul. 1968, *I. Markkanen s.n.* (H3151095–96); Eysturoy, 6°46′ W, 62°9′ N, 5 Jun. 1985, *J. Lewinsky 3763* (H), 6° 55′ W, 62°16′ N, 9 Jun. 1985, *J. Lewinsky 4510* (H); Kalsoy, 6°40′ W, 62°20′ N, 19 Jun. 1985, *J. Lewinsky 3638* (H); Stóra Dímun, 12 Aug. 1985, *B. Hammer s.n.* (H); Strömö, 8 Jul. 1973, *R. Fagerstén & M. Haapasaari 695* (H), *697* (H), *698* (H); Vágar, 7°13′ W, 62°02′ N, 23 Jun. 1985, *J. Lewinsky 3384* (H). FYN: Egebjärg, east of Bogense, 11 Jun. 1906, *A. Hesselbo s.n.* (H). NORDJYLLAND: Baggesvogn Skov, 31 Oct. 1946, *K. Holmen s.n.* (H). RIBE: Tondern an Baumslammen, Aug. 1893, *Prahe s.n.* (HBG).

Finland. ÅLAND: Bogskär, Oct. 1865, *J. O. Bomansson s.n.* (H); Eckerö, 30–31 Aug. 1892, *H. Lindberg s.n.* (H); Stackskär, 19 Jun. 1968, *C. A. Haeggström s.n.* (H); Stenbådan, 28 Jul. 1936, *O. Eklund s.n.* (H); Sottunga, 18 Jun. 1935, *O. Eklund s.n.* (H), 22 Jun. 1935, *s.n.* (H). CENTRAL FINLAND: Tammisaari, 29 Jun. 1898, *Ernst Häyrén s.n.* (H). SOUTHWEST FINLAND: Jurmo, Killingharu, 8 Jun. 1933, *O. Eklund* *s.n.* (H); Utö, Kårharu, 30 Jun. 1935, *O. Eklund s.n.* (H); Nötö, 11 Aug. 1936, *O. Eklund s.n.* (H). Uusimaa: Borgo, 30 Jun. 1859, *T. Saelan s.n.* (H); Ekenäs, 27 Jul. 1907, *J. S. W. Koponen s.n.* (H), 19 Aug. 1909, *Ernst Häyrén s.n.* (H), 26 Aug. 1934, *Hans Luther s.n.* (H); Tvärminne, 29 Jun. 1898, *Ernst Häyrén s.n.* (H), 19 Aug. 1899, *s.n.* (H), 15 Jul. 1907, *s.n.* (H), 15 Aug. 1907, *s.n.* (H), 22 Aug. 1907, *s.n.* (H), 7 Aug. 1908, *s.n.* (H), 6 Jul. 1909, *s.n.* (H), 2 Jul. 1914, *s.n.* (H), 6 Aug. 1920, *s.coll.* (H); 20 Jun. 1929, *Leo Pohjala s.n.* (H).

France. Bretagne: Finistère, 2 Jul. 1896, *Dismieiz s.n.* (NSW). Normandie: Cherbourg, *L. Corbière s.n.* (NSW).

Germany. Lower Saxony: Otterndorf, 17 Aug. 1825, *R. Timm s.n.* (HBG). Mecklenburg: Heiligendamm, Jun. 1908, *s.coll.* (HBG). Schleswig Holstein: s. loc., 27 May 1926, *illegible handwritten collector name* (HBG), 7 Apr. 1929, *Fuig Koppn.* (HBG); Nieblum, 11 Sep. 1824, *illegible handwritten collector name* (HBG).

Iceland. Snæfellsnes: 20 Jul. 1962, *B. Tohammssom s.n.* (H).

Ireland. Connacht: Drumcliffe, s. date, *Sprucei s.n.* (H). Leinster: Louth Co., Clogher Head, 16 Apr. 1965, *D. Synnott s.n.* (H), 29 Aug. 2007, *D. T. Holyoak 07-174* (BBSUK); Wicklow Co., Feathedber, 9 Jul. 1873, *S. O. Lindberg s.n.* (H). Munster: Muckross prope Killarney, s. date, *W. P. Schimper s.n.* (H); Cork Co., Knocknagree, 16 Sep. 1955, *s.coll.* (BBSUK).

Netherlands. Friesland: terr. Barradeel S. of village Minnertsga, Jul. 1978, *F. Sollman 78-8-25* (H).

Norway. Finnmark: Hammerfest, Sørøya, 7 Jul. 2010, *L. Hedenäs s.n.* (S). Hordalaud: Stord, Seuivik, 27 Aug. 1931, *M. J. Kotilainen s.n.* (H). Nordland: Tjotta, Trolaudet, Lõvogueset, 11 Jul. 1951, *M. J. Kotilainen s.n.* (H3151036–39); s. loc., 16–20 Jul. 1925, *s.n.* (H3150995–98). Rogaland: Stavanger, Jul. 1902, *N. Bryhn s.n.* (NSW766135, NSW766137). Sør-Trøndelag: Ladehammeren, 9 Jun. 1888, *I. Hagen s.n.* (NSW). Troms: Hindo, 17 Jul. 1916, *E. Häyrén s.n.* (H).

Sweden. Blekinge: Nättraby, 19 Aug. 1888, *H. W. Arnell s.n.* (H). Bohuslän: 24 Sep. 1926, *C. Stenholm s.n.* (H), Marstrand, Koön, Jul. 1889, *A. Arvén s.n.* (H). Skåne: s. loc., 31 Aug. 1915, *O. J. Hasslow s.n.* (H); s. loc., 1 Jul. 1931, *C. Stenholm s.n.* (MICH); s. loc., *L. J. Wahlstedt s.n.* (H); s. loc., 27 Jul. 1913, *H. Möller s.n.* (H); Stenshuvud, *A. Hovgard s.n.* (H, HBG, MICH). Södermanland: Utö, 22 May 2009, *L. Hedenäs s.n.* (S), 24 Jul. 2009, *L. Hedenäs s.n.* (S). Uppland: s. loc., 10 Jul. 1937, *A. Hülphers s.n.* (H); par. Rådmansö, 24 Jul. 1916, *H. W. Arnell s.n.* (HBG).

U.K. England: Cornwall, 1878, *R. V. Tellam s.n.* (NSW), Dec. 1883, *W. B. Waterfall s.n.* (NSW), Apr. 1862, *W. Curnow s.n.* (HBG); Flitwick Moor, 10 Sep. 2006, *T. L. Blockeel 35/233* (BBSUK). Northern Ireland: Western Co., Belmore Mt., 27 Feb. 1909, *W. N. Tetley s.n.* (BBSUK). Scotland: Arbroath, Mar. 1884, *W. Smith s.n.* (NSW); Argyllshire, 8 Jul. 1898, *H. M. Dixon s.n.* (NSW), *H. N. Qikon s.n.* (NSW); Fife Ness, Jun. 1905, *J. Mc. Andrew s.n.* (E); Fifesh, Wormit Bay, 3 May 1890, *G. Fotbes s.n.* (E); Island of May, Sep. 1885, *W. Evans s.n.* (E); Lanarkshire, Drumpellier County Park, 12 Nov. 2008, *D. F. Chamberlain s.n.* (BBSUK, E); Midlothian, Water of Leith, 13 Feb. 1999, *D. F. Chamberlain s.n.* (E), Bonnington Estate near Wilkieston, 29 May 2006, *D. G. Long 35659* (E), Side Moss, 28 May 2002, *E. M. Kungu S160* (E); Perth, near Skuan, 3 Jun. 1906, *T. H. R. s.n.* (NSW); near Brunton, 21 Nov. 2006, *D. F. Chamberlain & E. M. Kungu s.n.* (E).

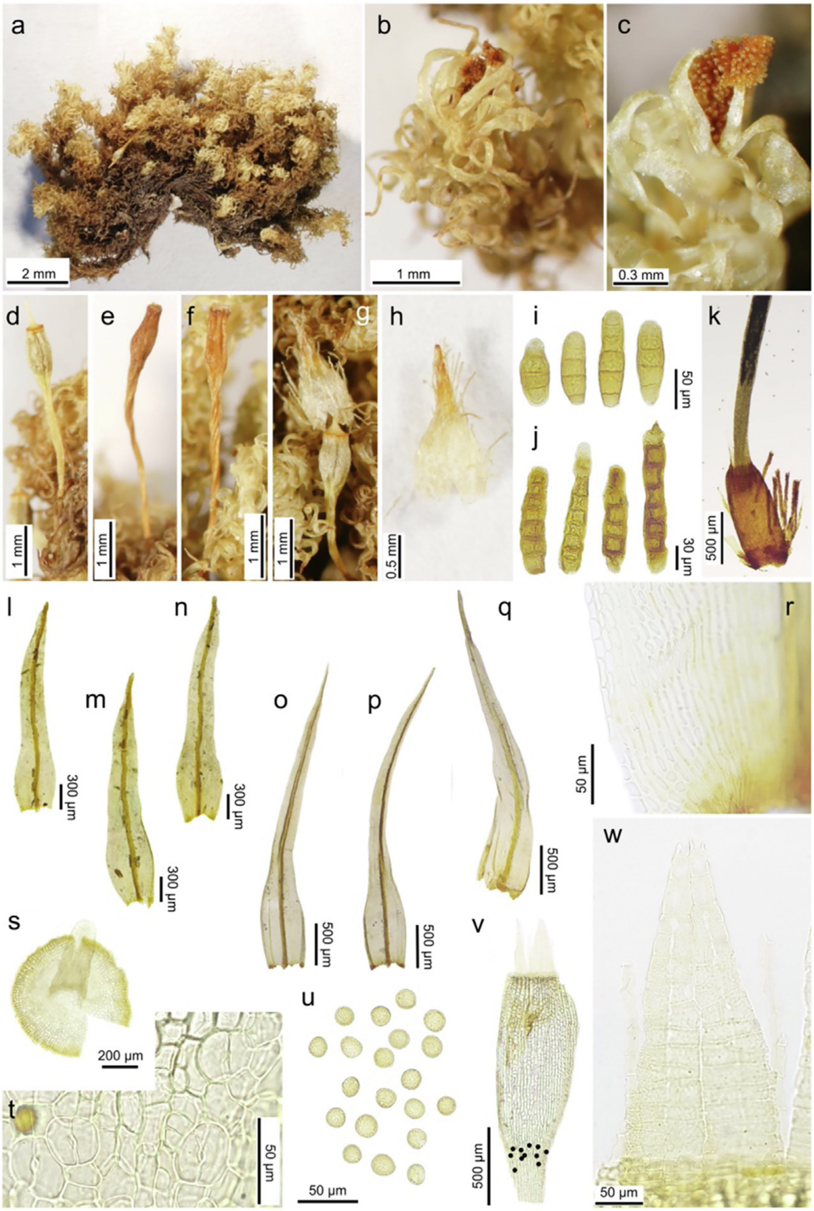


FIG. 142 – *Ulota phyllantha* Brid. a. Habit. b–c. Gemmae on leaf apex. d–f. Capsules in dry. g–h. Calyptra. i–j. Gemmae. k. Vaginula. l–p. Leaves. q. Perichaetial leaf. r. Marginal cells at leaf base. s. Operculum. t. Stomata. u. Spores. v. Exothecial wall, with dots indicating stoma position. w. Peristome. (All from *W. B. Schofield 100736* [non-type, DUKE] except c from *Timm* [non-type, HBG], j and l–n from *Roivainen s.n.* [non-type, MICH]).

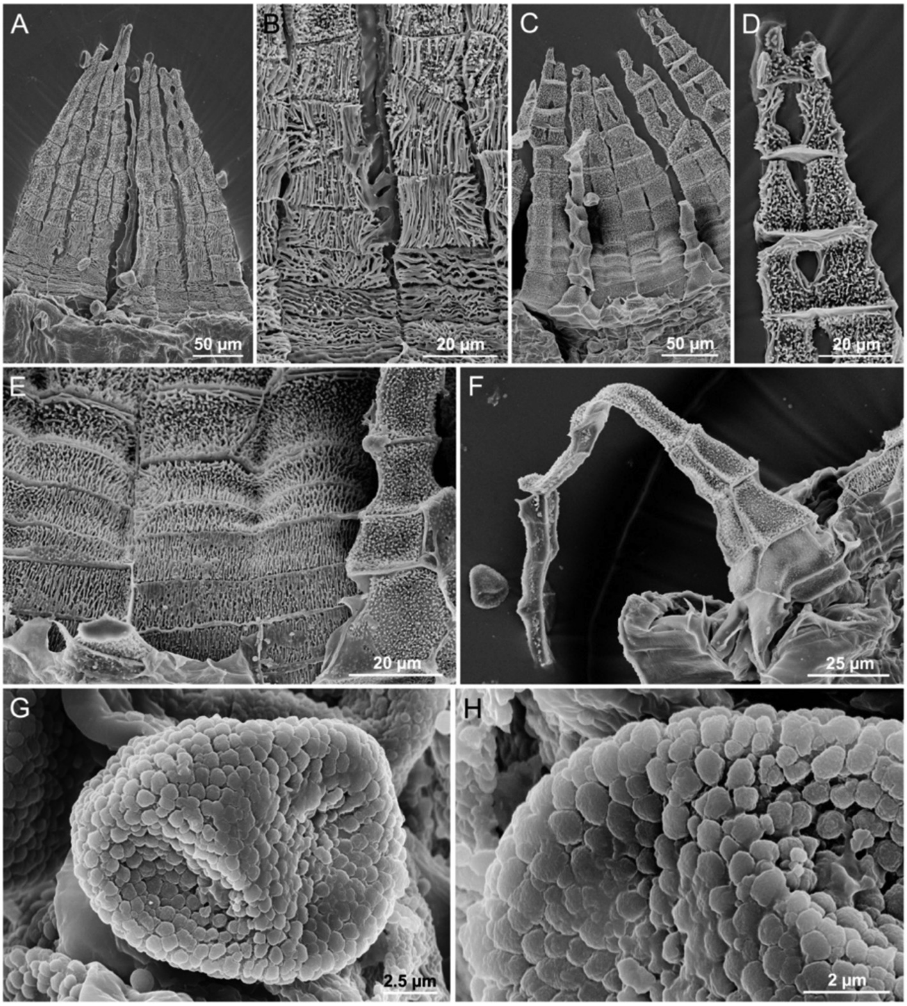


Fig. 143 – *Ulota phyllantha* Brid. A, outer surface of exostome; B, outer surface of basal exostome; C, inner surface of peristome; D, inner surface of upper exostome; E, inner surface of basal peristome; F, inner and outer surface of endostome; G, a spore; H, surface ornamentation of a spore. (All from *W. B. Schofield 100736* [non-type, DUKE]).

U.S.A. Alaska: Adak Island, 176°34′40″ W, 51°55′19″ N, 8 Aug. 2003, *W. B. Schofield 122288* (DUKE, H), 15–30 Jun. 1975, *D. K. Smith 3810* (MICH), 176° 39′31.8″ W, 51°45′40.6″ N, 22 Aug. 2006, *W. B. Schofield 125174* (UBC); Aleutian Islands, 2 Sep. 1949, *L. H. Jordal & H. A. Miller 3102* (MICH), 25 Jun. 1949, *T. P. Bank, Jr. 928* (MICH); Atka Island, 1 Jul. 1932, *W. J. Eyerdam 577* (MICH); Tagadak Island, 176°00′43.5″ W, 51°51′24.4″ N, 26 Aug. 2006, *W. B. Schofield 125320* (DUKE); Amchitka Island, 25 Nov. 1965, *H. T. Shacklette 7271* (MICH), *7273* (MICH), *7364* (MICH), *7507* (MICH); Cape Bartolome, 2 Jul. 1965,

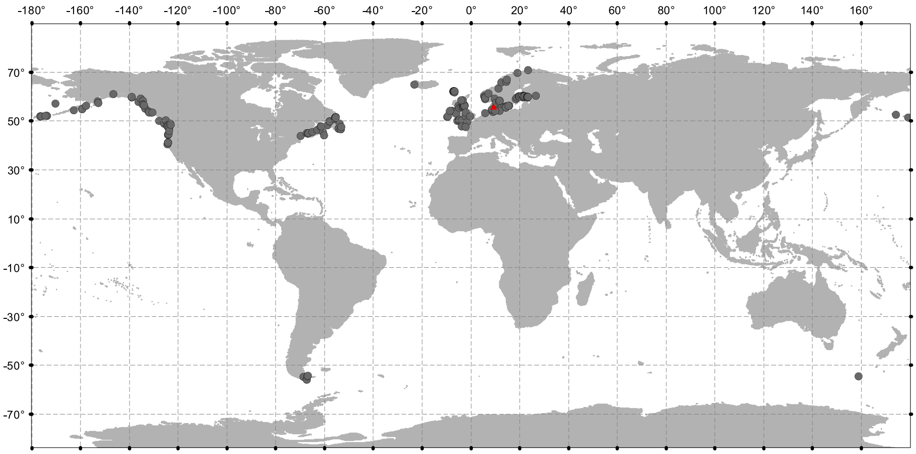


FIG. 144 – Distribution of *Ulota phyllantha* worldwide. The red triangle indicates the type locality.

A. Mathieson 205 (H); Eastern Pacific Coast Dsitrict, 7 Aug. 1967, *F. J. Hermann 22118* (H); Kuiu Island, 20 Aug. 1947, *W. J. Ryerdam 950* (MICH), *955* (MICH); near Haines, Sep. 1906, *J. B. Leiberg 1311* (MO); Nakchamik Island, 15 Jul. 1999, *W. B. Schofield 112889* (H); Raspbery Island, Port Nita, 20 Jun. 1939, *N. J. Eyerdam 527* (MICH); Pribilof Islands, 2 Aug. 1974, *L. Nagel s.n.* (MICH); Sanak Island, 162°42′42.7″ W, 54°23′58.3″ N, 3 Aug. 2006, *S. S. Talbot SAN-21* (UBC); Shemya Island, 174°07′ E, 52°43′ N, 26 Sep. 2002, *W. B. Schofield 120549* (DUKE); Shumagin Islands, 159°15′ W, 54°55′ N, 13 Jul. 1995, *W. B. Schofield 103767* (H), 11 Jul. 1996, *105891-2* (UBC); Washington Bay, 20 Aug. 1947, *W. J. Ryerdam 949* (MICH), 22 Sep. 1947, *977-2* (MICH); Yakobi Island, 18 Jun. 1957, *H. T. Shacklette 3982* (MICH); Yakutat, 19 Jul. 1945, *L. D. Stair* 4866 (MICH), 18 Jul. 1945, *4870* (MICH), 14 Jul. 1945, *4973* (MICH), 2 Jun. 1946, *H. S. Mazaika 5121* (MICH), *5122* (MICH), *5123* (MICH), *5124* (MICH). CALIFORNIA: Humboldt Co., 124°09′ W, 41°08′ N, 16 Jan. 1971, *D. H. Norris 11946* (MICH), *18862* (H), *23621* (MICH), *D. H. Vitt 7168* (H, MICH). MAINE: Sagadahoc Co., 17 Aug. 1986, *B. Allen 5017* (MICH); Washington Co., 6 Jul. 1902, *J. F. Collins 2629* (MICH). OREGON: Clatsop Co., 10 Jul. 1963, *F. J. Hermann 18680* (MICH); Waldport, 21 Jun. 1933, *T. C. Frye s.n.* (H, MICH); Yaquina Bay, *E. Hall s.n.* (MICH). WASHINGTON: Clallam Co., 5 May 1939, *A. H. Smith 13123* (MICH), 2 Jul. 1950, *A. L. Andrews 100* (MICH), *101* (MICH), 17 Jul. 1950, *102* (MICH); Grays Harbor Co., 14 Jul. 1950, *A. L. Andrews 108* (MICH); Jefferson Co., 24 Jun. 1964, *R. R. Ireland, Jr. 8907* (H, MICH); San Juan Island, 4 Oct. 1935, *C. C. Jao 270* (MICH). NEW BRUNSWICK: Albert Co., Fundy National Park, 6 Jul. 1968, *R. R. Ireland 11432* (MICH); Camponbello Island, Jul. 1902, *W. G. Farlow s.n.* (MICH); Charlotte Co., 19 Jul. 1970, *R. R. Ireland 13360* (MICH).

39. **Ulota pusilla** Malta, Acta Horti Bot. Univ. Latv. 2: 193. 1927. Type: Chile. Tierra del Fuego, Almirantazgo, 1908, *Halle & Skottsberg 460a* (holotype, H4334003! isotype, PC0099346!).

Ulota lativentrosa Müll. Hal. ex Malta, Acta Horti Bot. Univ. Latv. 2: 194. 1927. Type: Chile. Valdivia, Anden von Villarica, 1897, *D. Neger* (holotype, B; isotype, M0155421!). Proposed by Wang and Jia (2016).

Plants 0.5–1.5 cm tall, green above, gradually brown below. Stems somewhat slender. Leaves flexuose, rarely crisped when dry, erect-spreading to patent when moist, (1–) 1.3–1.5 (–1.7) mm long; leaf lamina lanceolate, unistratose; leaf base very wide, rounded, concave; apex long acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (6–) 8–11 (–15) × (6–) 8–10 (–13) μm, thick-walled, with (1–) 2–4 low, rarely tall papillae per cell, sometimes branched; basal inner cells linear, elongate-rectangular, (15–) 22–31 (–42) × (1–) 2–3 (–5) μm, with thick wall, smooth; basal marginal cells differentiated in 5–10 rows, hyaline, quadrate to rectangular, with thin, sometimes transversely slightly thickened walls.

Autoicous. Perichaetial leaves hardly differentiated, 1.6–1.7 mm. Vaginula is naked. Seta (2.5–) 2.6–3.2 mm long, twisted anticlockwise when dry. Capsule long exserted, 1–1.5 mm long. Urn cylindrical, hardly or slightly, rarely moderately constricted below the mouth when dry and empty, eight furrows almost along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, scattered on the urn. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, revolute when dry, often lying on the exothecium, lanceolate, densely and strongly papillose or striate-papillose at the apex on the outside, striate or striate-papillose at the apex on the inside. Endostome segments 16, sometimes alternatively 8 long 8 short, and the short ones often fugacious, linear to narrow-lanceolate, ≥2/3 height of teeth, uniseriate or rarely partially biseriate, 1/2–1/4 width of teeth, yellowish, smooth on the outside, distinctly finely papillose or sinuously striate on the inside. Opercula yellowish, with a short to medium long beak. Calyptra mitrate, sparsely to densely hairy. Spores spherical, finely papillose, (21–) 25–35 (–43) μm in diameter.

Illustration: Malta (1927) and Wang and Jia (2016); figures 145 and 146.

Habitat: It grows on tree trunks, but no phorophyte was recorded. There is only one altitude record, at 1420 m. It occasionally grows mixed with *Ulota macrocalycina* and *U. magellanica*.

Distribution: It occurs in the southern part of Chile and Argentina. Figure 147.

Notes: *U. pusilla* is characteristic of 16 yellowish endostome segments with distinctly papillose or striate and can be distinguished from other congeners by combining the non-crisped leaves, many rows of hyaline thin-walled cells at basal leaf margins, hardly or slightly constricted capsules and stomata located on the urn.

In *Ulota*, the ornamentation of broad endostome segments is often stronger than that of narrow endostome segments. The narrow endostome segments are generally

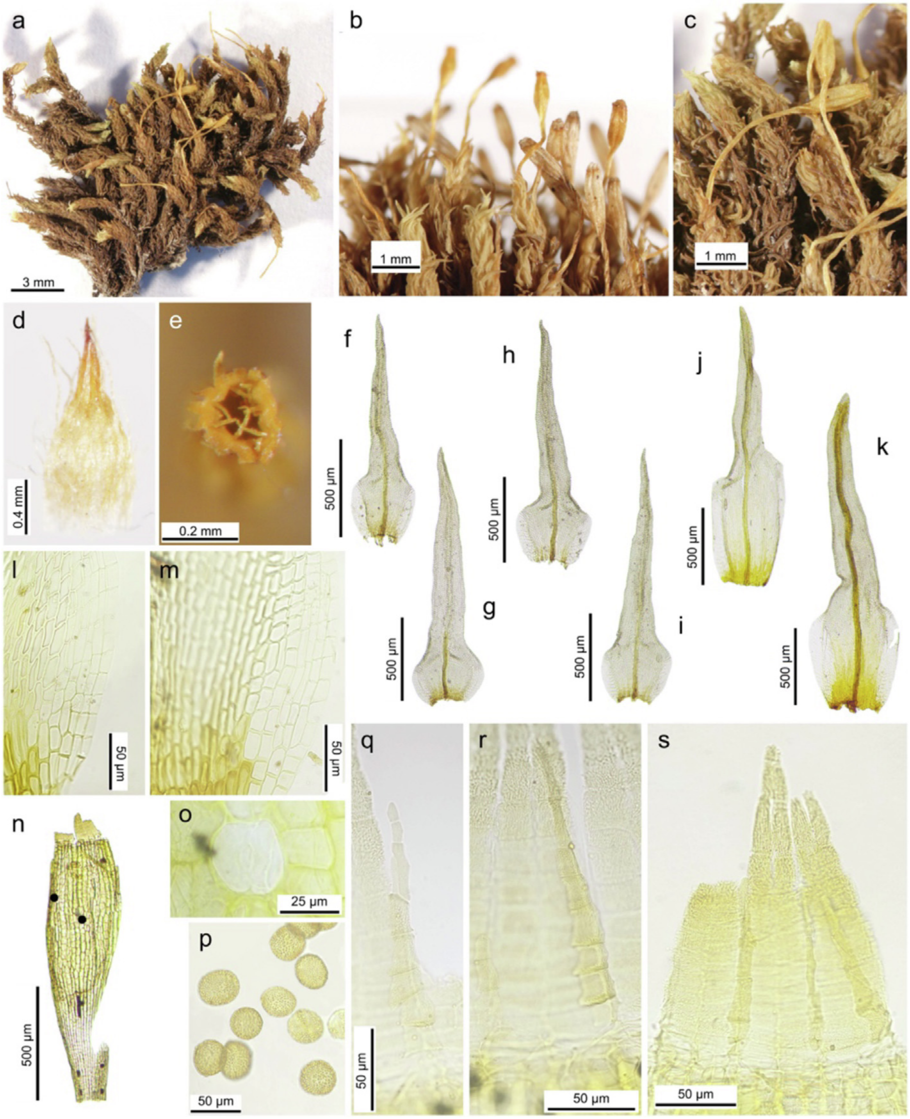


FIG. 145 – *Ulota pusilla* Malta. a. Habit. b–c. Capsules in dry and empty. d. Calyptra. e. Capsule mouth viewed from above. f–i. Leaves. j–k. Perichaetial leaves. l–m. Marginal cells at leaf base. n. Exothecial wall, with dots indicating stoma position. o. Stoma. p. Spores. q–r. Endostome segments. s. Peristome. (b, d–i, l and m, p, s from *T. Halle et C. Skottsberg* [non-type, S], k, j, n, o from holotype in H, a and c from *B. Ruthsatz s.n.* [non-type, H], q and r from *R. Thaxter 216* [non-type, PC]).

slightly coarse on the inside, few species are smooth, and few species are densely papillose, such as *Ulota delicata*, *U. macrodontia*, and *U. pusilla*. The Chinese *Ulota delicata* and *U. pusilla* both have 16 endostome segments, but the former differs in the

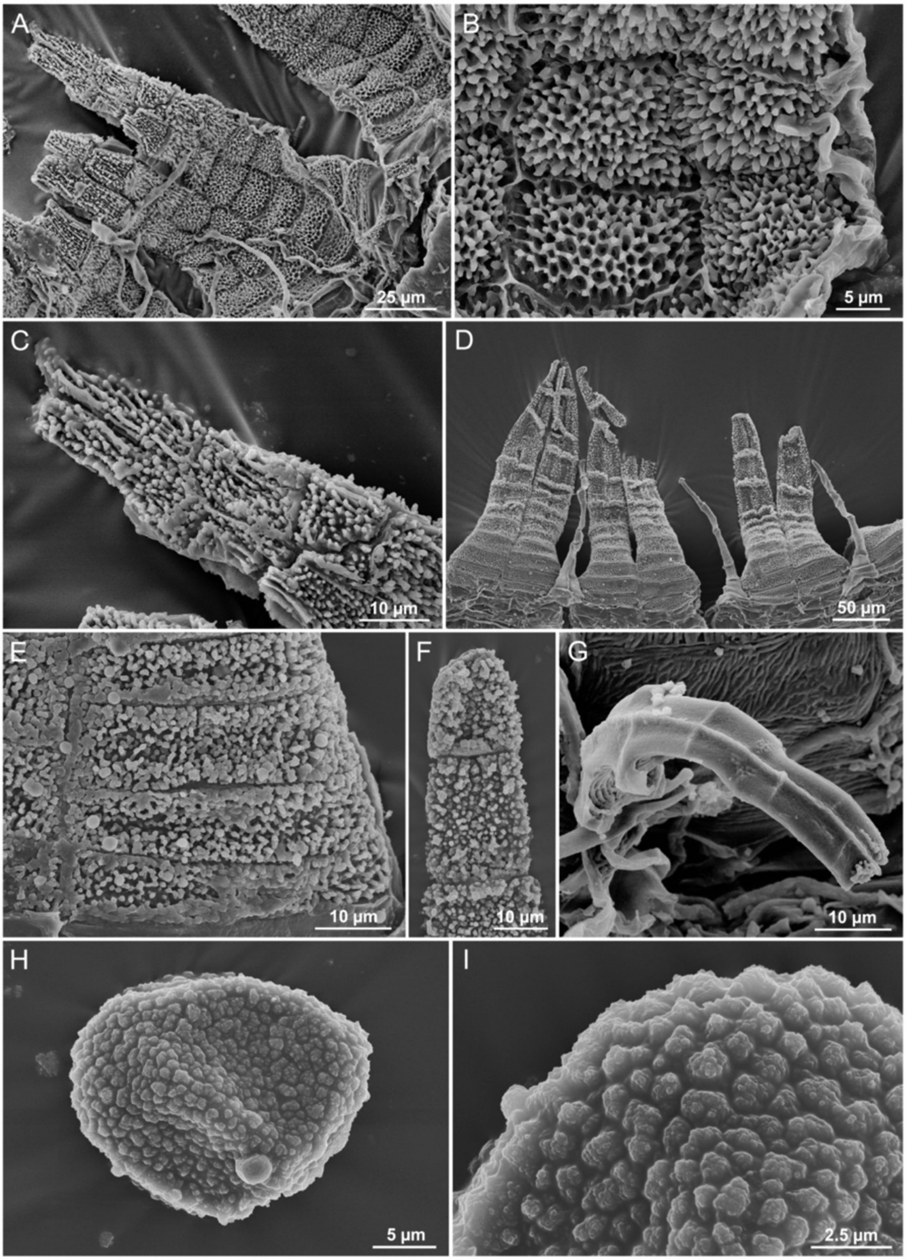


FIG. 146 – *Ulota pusilla* Malta. A, outer view of exostome; B, outer surface of basal exostome; C, outer surface of upper exostome; D, inner view of peristome; E, inner surface of basal exostome; F, inner surface of upper exostome; G, outer surface of endostome; H, a spore; I, surface ornamentation of a spore. (A–C and G from holotype in H, others from *B. Ruthsatz s.n.* [non-type, H]).

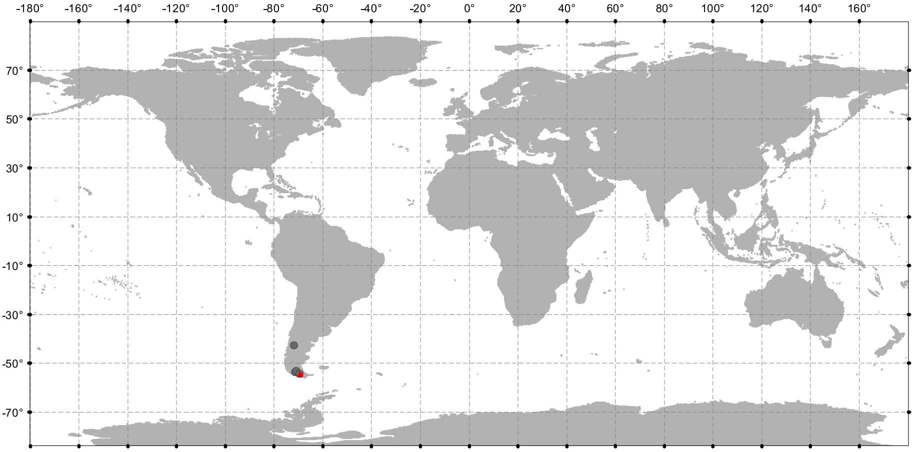


FIG. 147 – Distribution of *Ulota pusilla* worldwide. The red triangle indicates the type locality.

strongly crisped leaves, hyaline leaf cells with conspicuously thickened transverse walls, capsules often puckered at mouth and stomata located at the transition zone between urn and neck. In fact, *Ulota pusilla* is very similar to the local species *U. macrodontia*, and both share in the hardly constricted capsules, urn-located stomata, distinctly ornamentated endostome segments, and hairy calyptra. However, the latter differs in eight endostome segments with extremely strongly papillose, strongly flexuose to slightly crisped leaves with relatively narrow bases which differentiated in less rows (4–6) of hyaline cells at margins with equally slightly thickened walls.

Key to *Ulota pusilla* and its closely related species.

1. Leaves strongly crisped when dry; hyaline cells at leaf basal margins with distinctly thickened transverse walls; capsules often obviously puckered at mouth when dry; stomata located at the transition zone between urn and neck.. *U. delicata*
1. Leaves erect, flexuose to slightly crisped when dry; hyaline cells at leaf basal margins with thin or equally slightly thickened walls; capsules never puckered at mouth when dry; stomata located on the urn..2
2. Endostome segments 8, strongly papillose as much as exostome teeth; leaves moderately crisped when dry; leaf bases relatively narrow, with less rows (4–6) of hyaline cells at margins, with equally slightly thickened walls.. *U. macrodontia*
2. Endostome segments 16, distinctly papillose or striate but weaker than exostome teeth; leaves flexuose, rarely crisped when dry; leaf bases very wide, with more rows (5–10) of hyaline cells at margins, with thin or sometimes transversely slightly thickened walls... *U. pusilla*

Additional Specimens Examined: **Argentina**. Chubut: Lago Menéndez, 21 Jan. 1938, *A. Kalela B248j(1)* (H).

Chile. Bío bío: De Valdivia, Volcán Villarica, Jan. 1966, *B. Ruthsatz s.n.* (H3150923–24). Magallanes: Brunswick, 3 Jun. 1908, *T. Halle 459* (PC); Punta Arenas, Feb. 1906, *R. Thaxter 216* (PC); Tierra del Fuego, Almirantazgo, 2 Mar. 1908, *T. Halle & C. Skottsberg s.n.* (S), 9 Mar. 1908, *460-2* (PC).

40. **Ulota pycnophylla** Dusén ex Malta, Acta Horti Bot. Univ. Latv. 2: 183. f. 6. 1927. Type: Chile. Cordillera de la Costa, Angol, an Stämmen, elev. 700 m, 4 Nov. 1896, *P. Dusén 346b* (holotype, S-B115596!).

Ulota aurantiaca Dusén ex Malta, Acta Horti Bot. Univ. Latv. 2: 184. f. 7. 1927. Type: Chile. Patagonia, 21 Nov. 1895, *P. Dusén 15a* (holotype, S-B88537!). Proposed by Wang and Jia (2016).

Plants less than 1 cm tall, green above, brown below. Stems usually branched. Leaves erect-appressed, sinuose or slightly flexuose when dry, erect-spreading when moist, (1–) 1.1–1.5 (–1.6) mm long; leaf lamina lanceolate, unistratose; leaf base wide, ovate; apex acute to acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, oblong, (6–) 8–9 (–12) × (5–) 6–7 (–8) μm, thick-walled, almost smooth or with short papillose; basal inner cells linear, elongate-rectangular, (17–) 25–31 (–39) × (4–) 6–7 (–8) μm, with strongly thickened wall, smooth; basal marginal cells differentiated in 5–10 rows, hyaline, quadrate to rectangular, with thin, sometimes slightly transversely thickened walls.

Autoicous. Perichaetial leaves much longer, (1.6–) 1.8–2.3 (–2.4) mm. Vaginula not seen. Seta ca. 2 mm long, sometimes twisted anticlockwise when dry. Capsule long exserted, (1.3–) 1.4–2 (–2.4) mm long. Urn cylindrical, moderately to strongly constricted below the mouth when dry and empty, with eight furrows almost along the entire length, with prominent ribs alternately. Neck short, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, revolute when dry, often lying on the exothecium, lanceolate, densely papillose on the outside, papillose-striate on the inside. Endostome segments 8, narrow-lanceolate, ≥2/3 height of teeth, uniseriate or irregularly biseriate at the base, ca. 1/4 width of teeth, hyaline, smooth outside, slightly coarse inside. Opercula yellowish, with a short beak. Calyptra mitrate, densely hairy. Spores spherical, finely papillose, (22–) 24–27 (–32) μm in diameter.

Illustration: Malta (1927) and Wang and Jia (2016); figure 148.

Habitat: There are no relevant records in specimens and literature except for one altitudinal record from the holotype, 700 m.

Distribution: It is **endemic** to Chile. Figure 149.

Notes: We hitherto have only seen the type collections of *Ulota pycnophylla*. It is diagnostic of the erect or slightly flexuose leaves, conspicuously differentiated cells at

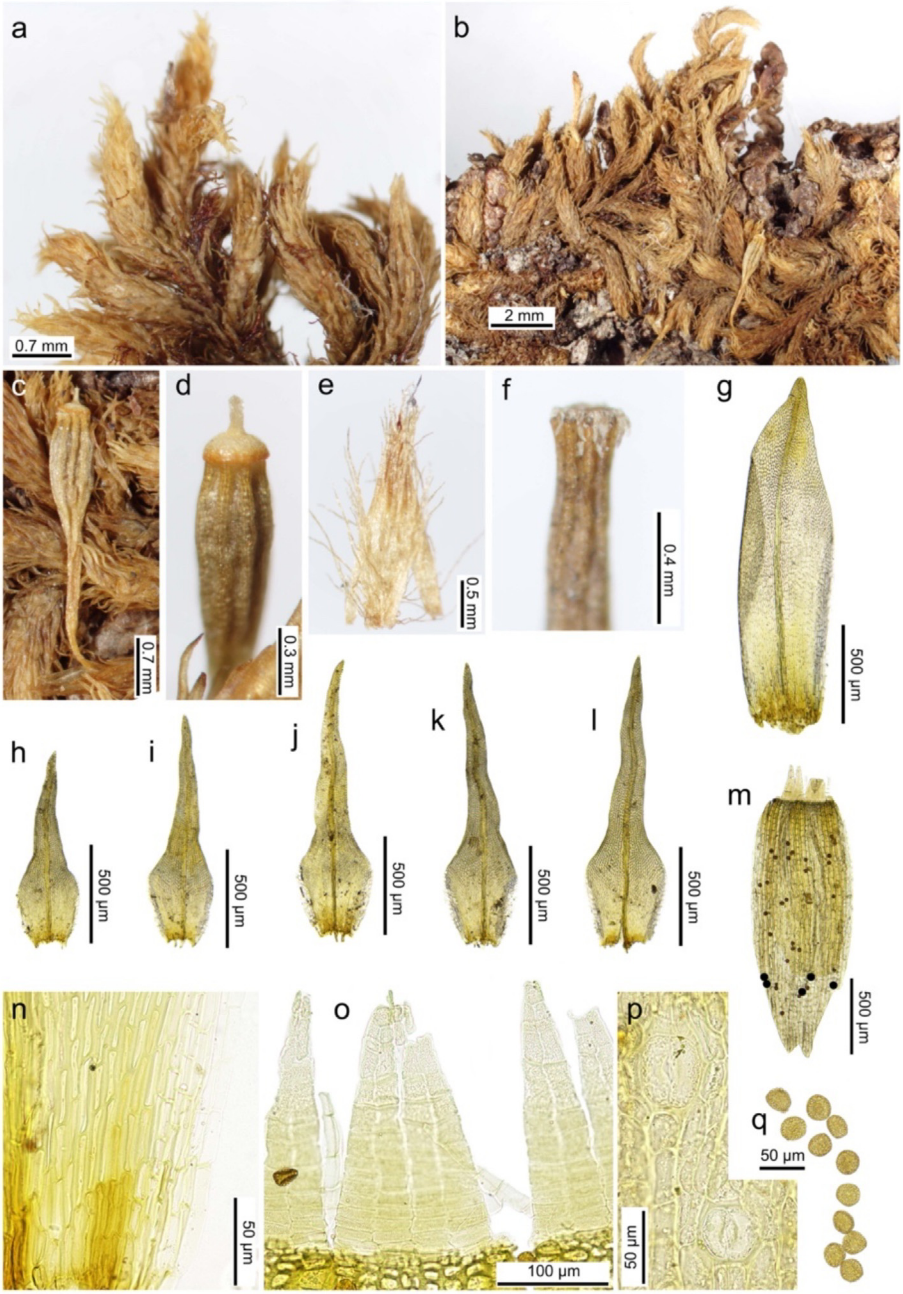


FIG. 148 – *Ulota pycnophylla* Dusén ex Malta. a–b. Habit. c–d. Capsules in dry. e. Calyptra. f. Capsule mouth viewed from the side. g. Perichaetial leaf. h–l. Leaves. m. Exothecial wall, with dots indicating stoma position. n. Marginal cells at leaf base. o. Peristome. p. Stomata. q. Spores. (All from the holotype in S except e and f from the holotype of *U. aurantiaca* in S).

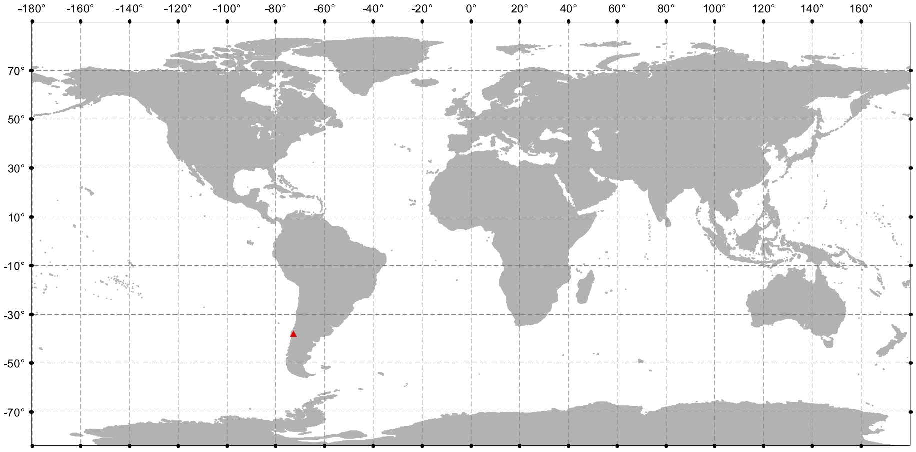


FIG. 149 – The type locality of *Ulota pycnophylla*.

basal leaf margins, stomata on the transition zone of the urn and neck, and densely hairy.

Ulota pycnophylla is one of the few species in the genus *Ulota* with many rows of hyaline cells with thin walls at basal leaf margins. At present, only four species worldwide have this feature, and their differences have been discussed in detail in Notes of *Ulota macrocalycina*. Among them, *Ulota pycnophylla* is most related to *U. macrocalycina*. Both often have erect leaves, ovate leaf base, distinctly constricted capsules, and eight narrow endostome segments. *Ulota macrocalycina*, however, is distinguished by the leaves with acute apex, the stomata often occur on the urn, the papillose (no striate) exostome teeth, the naked calyptra and the relatively larger spores (29–33 μm).

Key to *Ulota pycnophylla* and its closely related species.

1. Leaf apex acute; stomata often on the urn; calyptra always naked; exostome teeth with densely papillose inside; spores relatively larger, 29–33 μm.. *U. macrocalycina*
1. Leaf apex often acuminate; stomata on the transition zone between urn and neck; calyptra densely hairy; exostome teeth with papillose-striate inside; spores small, 24–27 μm.. *U. pycnophylla*

Additional Specimens Examined: None.

41. ULOTA REHMANNII Jur., Verh. Zool.-Bot. Ges. Wien 14: 191. 1864. ≡ *Orthotrichum rehmannii* (Jur.) Kindb., Eur. N. Amer. Bryin. 2: 307. 1897. TYPE: POLAND. Tatra Mountains, "Auf Stämme und Aesten der Nadelbäume bei Jako-pave: Tatragebirge", *A. Rehmann s.n.* (holotype, M-0138781! isotype, BP!).

Plants 0.5–2 cm tall, yellow on the top, gradually dark below. Stems usually branched. Leaves flexuose, rarely crisped when dry, patent when moist, (1.2–) 1.3–1.7 (–2) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex acute to acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, oblong, (6–) 8–12 (–16) × (3–) 5–8 (–11) μm, thick-walled, smooth or with low papillose; basal inner cells linear, rhomboidal, rectangular, elongate-rectangular, (12–) 21–28 (–36) × (1–) 3–5 (–7) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in (2–) 4–6 (–9) rows, hyaline, quadrate to rectangular, with transversely thickened walls.

Autoicous. Perichaetial leaves somewhat longer, (1.9–) 2–2.2 (–2.4) mm. Vaginula is naked or hairy. Seta (1.5–) 2–3.3 (–4) mm long, sometimes twisted anticlockwise when dry. Capsule short to long exserted, 1–1.2 (–1.3) mm long. Urn short-cylindrical, sometimes funnel-shaped, hardly, sometimes moderately constricted below the mouth when dry and empty, with eight furrows almost along the entire length, with prominent ribs alternately. Neck short, gradually narrowed to the seta. Exothecial cells differentiated into eight bands, almost as long as an urn, two to three cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, reflexed when dry, often lying on the exothecium, lanceolate, sometimes semitransparent above, strongly striate that variably orientated, and partially papillose outside, finely papillose and striate inside. Endostome segments 8, linear, rarely narrow-lanceolate, as long as teeth, uniseriate, 1/3–1/4 width of teeth, hyaline or yellowish, smooth outside, slightly scabrous to finely papillose inside. Opercula yellowish, with a short beak. Calyptra mitrate, naked or sparsely hairy. Spores spherical, finely papillose, (23–) 28–32 (–36) μm in diameter.

Illustration: Ignatov and Ochyra (1994), Sotiaux and Sotiaux (1999) and Wang and Jia (2012a); figures 150 and 151.

Habitat: It grows on trunks and branches of trees, such as *Abies* and *Sorbus*. There are a few records of altitude: 200–1940 m. No mixed growth has been found in this study, but it was mentioned in a previous study (Fedosov and Ignatova, 2018) that it was often mixed with *Ulota intermedia*.

Distribution: It sporadically occurs in the cool temperate area of Eurasia. It is also reported from Turkey, Altai Mts, and the Caucasian region (Fedosov and Ignatova, 2018; Lara *et al.*, 2010; Chikovani and Svanidze, 2004; Ignatov and Ochyra, 1994). Figure 152.

Notes: *Ulota rehmannii* is characteristics by strongly striolate exostome teeth and sparsely hairy or naked calyptra. The latter character is rare within *Ulota* and present in four species so far, including *U. japonica* from East Asia, *U. magellanica* from South America, *U. yunnanensis* from China, and *U. rehmannii*. However, *Ulota japonica* can be distinguished by capsules strongly constricted when dry, exostome teeth with densely papillose or slightly striate near the apex, more rows of hyaline cells at basal leaf margins (6–10 rows), and small spores (19–22 μm); *U. magellanica* by the erect, sinuose and falcate leaves, weakly differentiated cells at basal leaf margins, capsules strongly constricted when dry, 16 wide endostome

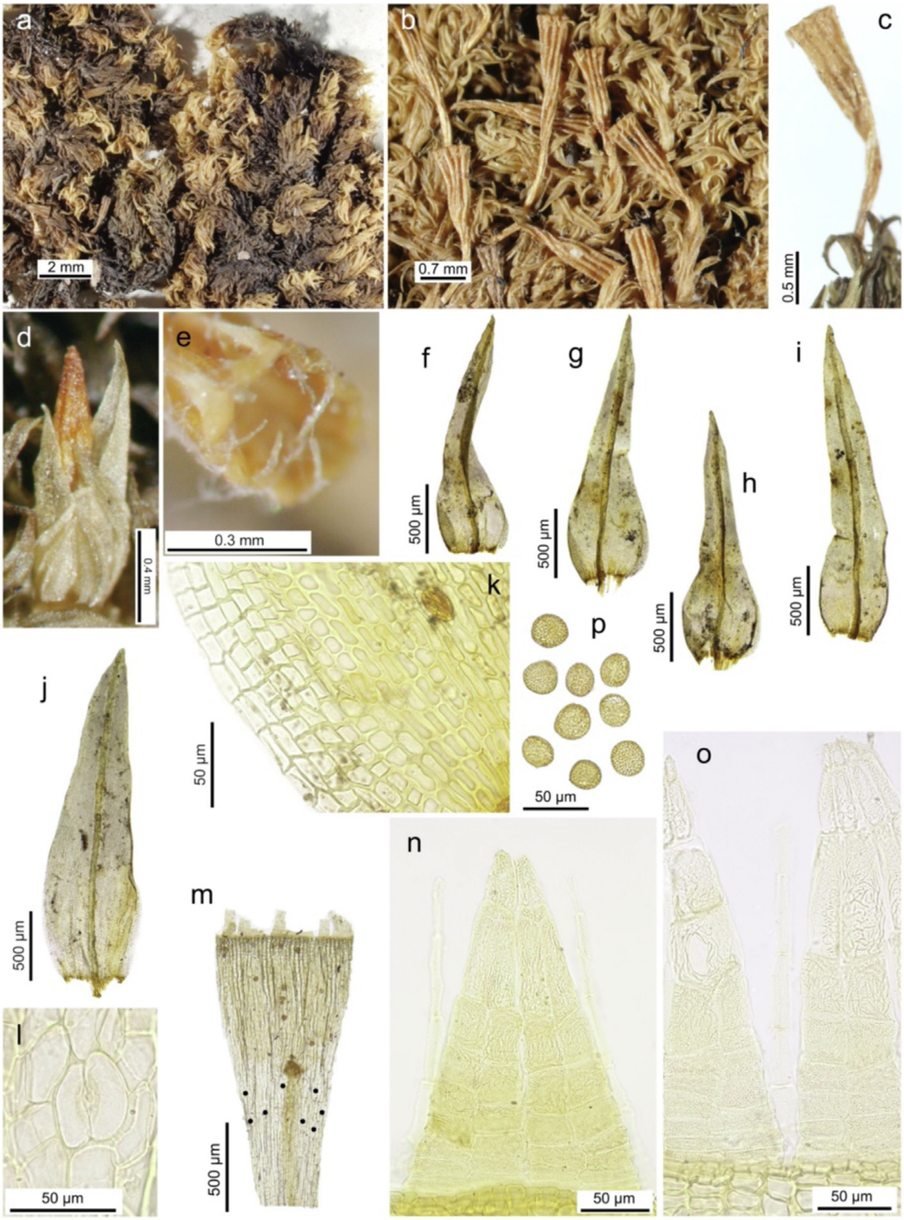


FIG. 150 – *Ulota rehmannii* Jur. a–b. Habit. c. A capsule in dry and empty. d. Calyptra. e. Capsule mouth viewed from above. f–i. Leaves. j. Inner perichaetial leaf. k. Marginal cells at leaf base. l. Stoma. m. Exothecial wall, with dots indicating stoma position. n–o. Peristome. p. Spores. (a, d, l, o and p from *h3227* [non-type, BP], c and m from *8hii* [non-type, BP], b and e from *h3224* [non-type, BP] and f–k and n from *Q. Gao 7507* [non-type, IFP]).

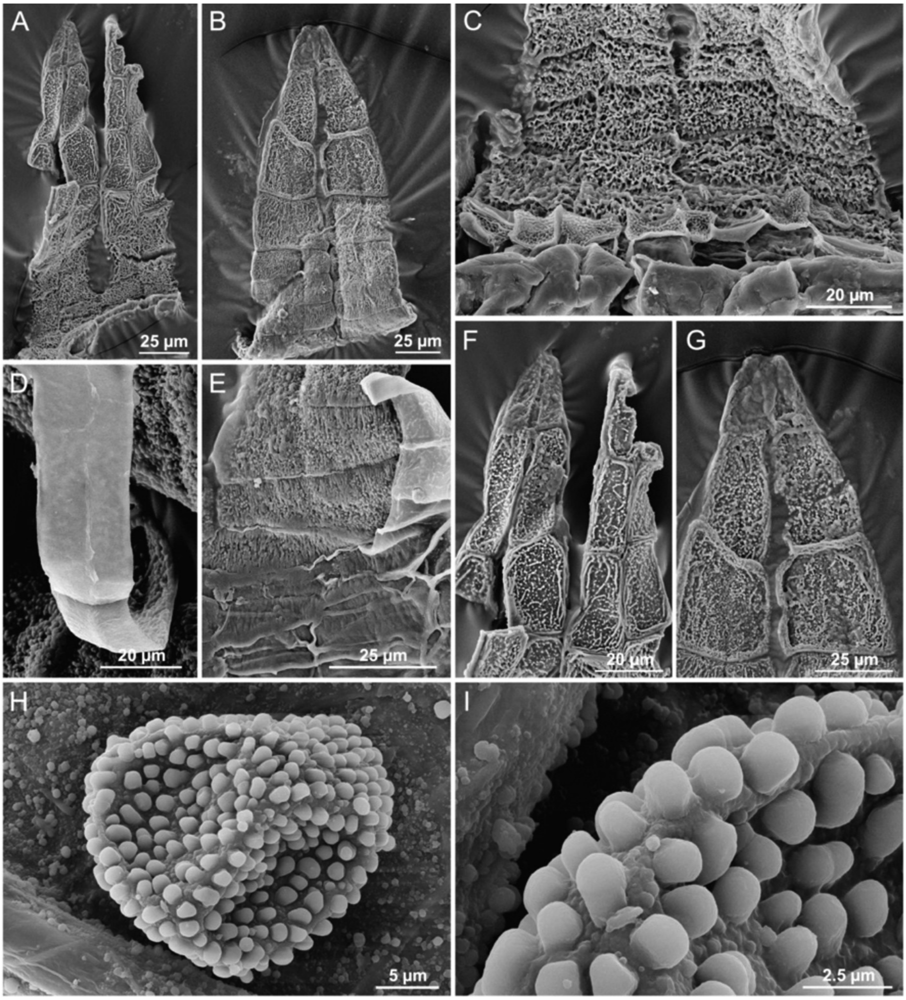


FIG. 151 – *Ulota rehmannii* Jur. A, outer view of exostome; B, inner view of exostome; C, outer surface of basal exostome; D, outer surface of endostome; E, inner surface of basal peristome; F, outer surface of upper exostome; G, inner surface of upper exostome; H, a spore; I, surface ornamentation of a spore. (All from *J. Breiveer* [non-type, HBG]).

segments and large spores (36–44 μm); *U. yunnanensis* by the multicellular spores (50–65 μm), strongly crisped leaves and weakly differentiated cells at basal leaf margins.

Locally, *Ulota rehmannii* resembles *U. reptans* in usually flexuose leaves, short-cylindrical capsules that hardly constricted when dry, and eight narrow endostome segments. But in *U. reptans*, the leaf cells at basal margins are weakly differentiated, exostome teeth are never strongly striolate, calyptra is never naked, and spores are relatively large (30–38 μm).

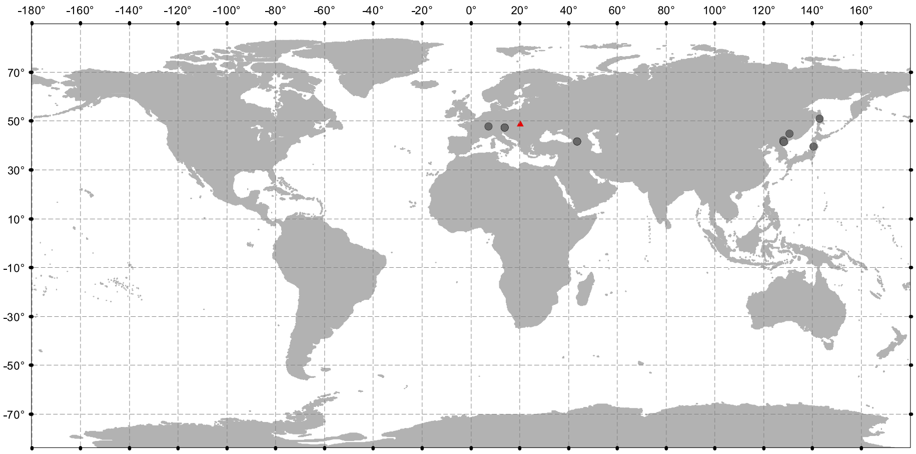


FIG. 152 – Distribution of *Ulota rehmannii* worldwide. The red triangle indicates the type locality.

The hairiness of calyptra in *U. rehmannii* is rarely dense, and it happened in two cases (*J. Breidter s.n.*, PC; *V. Y. Cherdantseva s.n.*, PE) in this study.

Key to *Ulota rehmannii* and its closely related species.

1. Spores multicellular, 46–71 μm; leaves strongly crisped when dry..*U. yunnanensis*
1. Spores unicellular, 19–44 μm; leaves erect to flexuose when dry......................2
2. Endostome segments 16, lanceolate...*U. magellanica*
2. Endostome segments 8, linear to narrow-lanceolate...3
3. Capsules strongly constricted when dry; leaf cells at basal margins obviousely differentiated in 6–10 rows; plants small, 0.5–1 cm; leaves longer, 1.7–2.2 mm; spores small, 19–22 μm..*U. japonica*
3. Capsules hardly to moderately constricted when dry; leaf cells at basal margins weakly differentiated or distinctly differentiated in 4–6 rows; plants relatively large, 0.5–2 cm; leaves short, 1.3–1.7 mm; spores relatively large, 28–38 μm..4
4. Leaf cells at basal margins weakly differentiated, no more than three rows; exostome teeth densely papillose outside; spores relatively large, 30–38 μm..*U. reptans*
4. Leaf cells at basal margins distinctly differentiated in 4–6 rows; exostome teeth prominently variably striate outside; spores small, 28–32 μm........*U. rehmannii*

Additional Specimens Examined: **Austria**. STYRIA: Schladming, 25 July 1870, *J. Breidter s.n.* (H, HBG, PC), Jul. 1870, *J. Breidter s.n.* (PC), s. date, *s.coll.* (PC).

China. Heilongjiang: Muling Co., Jul. 1977, *Q. Gao 13644* (IFP). Jilin: Changbai Mt., 25 Aug. 1963, *Q. Gao 7507* (IFP), 31 Aug. 1963, *7600* (IFP), Antu Co., 24 Sep. 1981, *T. Koponen 37110* (IFP).

France. Grand Est: Vosges Mts, 3 Aug. 1883, *s.coll.* (NSW).

Georgia. Bakuriani: s. loc., 20 Apr. 1916, *Kozlowsry s.n.-2* (H), 28 Jun. 1916, *J. A. Leptšenko s.n.-2* (H).

Japan. Akita: Kyowa, 9 Jun. 1990, *Takahashi YT-10193* (AKPM).

Russia. Sakhalin: Sakhalin Island, 142°46′7″ E, 50°55′36″ N, 6 Aug. 2001, *V. Y. Cherdantseva s.n.* (PE).

42. **Ulota reptans** Mitt., Trans. Linn. Soc. London, Bot. 3: 161. 1891. Type: Japan. Fujisan, May 1887, *J. Bisset s.n.* (isotype, NICH! E00052662!).

Plants 1–1.5 cm tall, slender, yellow on the top, brown to black below. Stems somewhat slender, usually branched. Leaves erect to flexuose when dry, patent when moist, (0.9–) 1.3–1.6 (–1.7) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex acute to acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells rounded, hexagonal, oblong, (5–) 8–11 (–15) × (4–) 7–8 (–10) μm, thick-walled, with low papillose; basal inner cells rhomboidal, linear and rectangular, (14–) 20–27 (–35) × (1–) 2–6 (–7) μm, with moderately thickened wall, smooth; basal marginal cells weakly differentiated, no more than three, rarely up to five rows, hyaline, quadrate to rectangular, with transversely thickened walls.

Autoicous. Perichaetial leaves hardly differentiated, (1.2–) 1.4–1.6 mm. Vaginula is naked or hairy. Seta 2.5–3.2 (–3.3) mm long, twisted anticlockwise when dry. Capsule short to long exserted, 1.2–1.4 mm long. Urn short-cylindrical, hardly constricted below the mouth when dry and empty, eight furrows almost along the entire length, with prominent ribs alternately. Neck short, gradually narrowed to the seta. Exothecial cells differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the base of the urn or the junction between the urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, reflexed when dry, often lying on the exothecium, lanceolate, densely papillose below and striate-papillose at the apex outside, finely papillose or papillose-striate inside. Endostome segments 8, linear, ≥2/3 height of teeth, uniseriate, ca. 1/4 width of teeth, hyaline or yellowish, smooth outside, nearly smooth or finely papillose inside. Opercula not seen. Calyptra mitrate, sparsely, rarely moderately hairy. Spores spherical, finely papillose, (20–) 30–38 (–43) μm in diameter.

Illustration: Noguchi (1939), Noguchi and Iwatsuki (1989) and Wang and Jia (2012a); figures 153–155.

Habitat: It grows on trunks of the tree, such as *Abies* and conifers. There are some records of altitude: (1960–) 2000–2300 (–2900) m. It is occasionally mixed with *U. crispa*.

Distribution: It is known from Japan. It is reported recently from Russian Far East (Fedosov and Ignatova, 2018), but we have not seen any specimens yet. Figure 156.

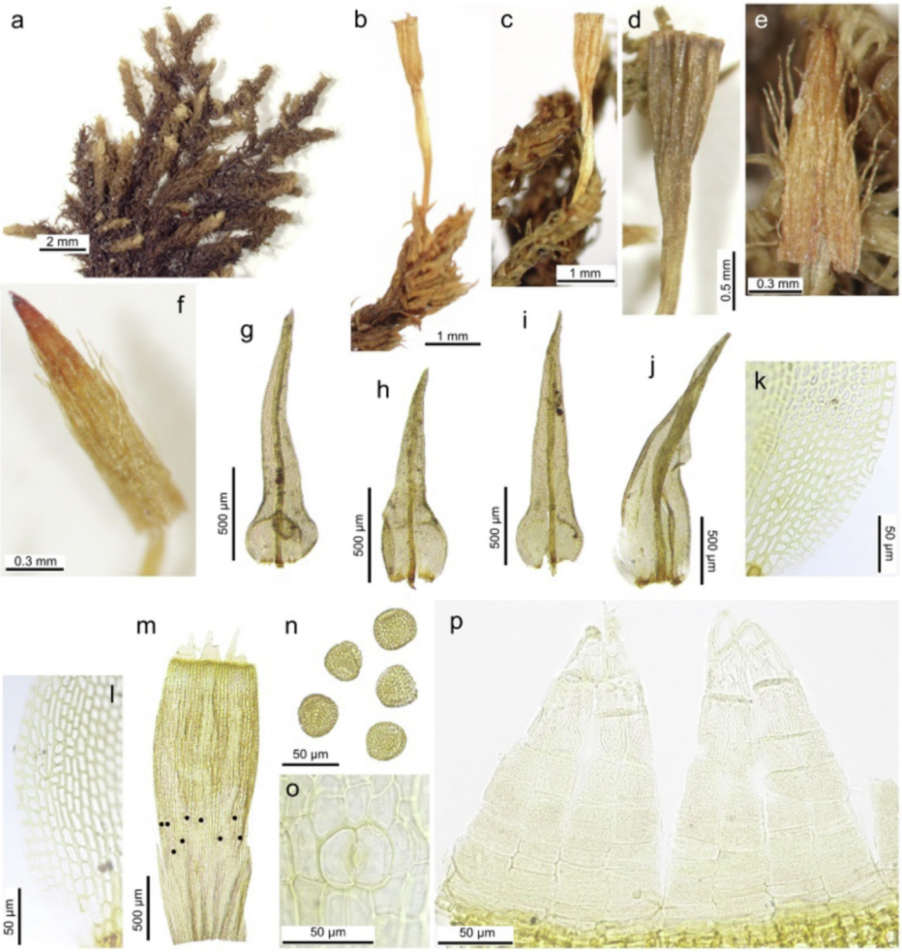


FIG. 153 – *Ulota reptans* Mitt. a. Habit. b–d. Capsules in dry and empty. e–f. Calyptra. g–i. Leaves. j. Inner perichaetial leaf. k–l. Marginal cells at leaf base. m. Exothecial wall, with dots indicating stoma position. n. Spores. o. Stoma. p. Peristome, with endostome segments caducous. (a–f from *Z. Iwatsuki* [non-type, S], g–m, o from isotype in E, n, p from *S. Nakanishi s.n.* [non-type, HYO]).

Notes: The first impression of *Ulota reptans* are its very slender plants and much smaller leaves. As mentioned above (see Notes in *U. megalospora*), besides *U. reptans*, species with the smallest leaves in *Ulota* include *U. gigantospora* from China, *U. macrocalycina* from South America and *U. megalospora* from North America. However, *Ulota gigantospora* differs in crisped leaves and multicellular spores (87–105 μm), *U. macrocalycina* in leaves with acute apex, hyaline cells at basal leaf margins differentiated in 4–10 rows, capsules strongly constricted when dry, stomata confined to the urn and always naked calyptra and *U. megalospora* in capsules with

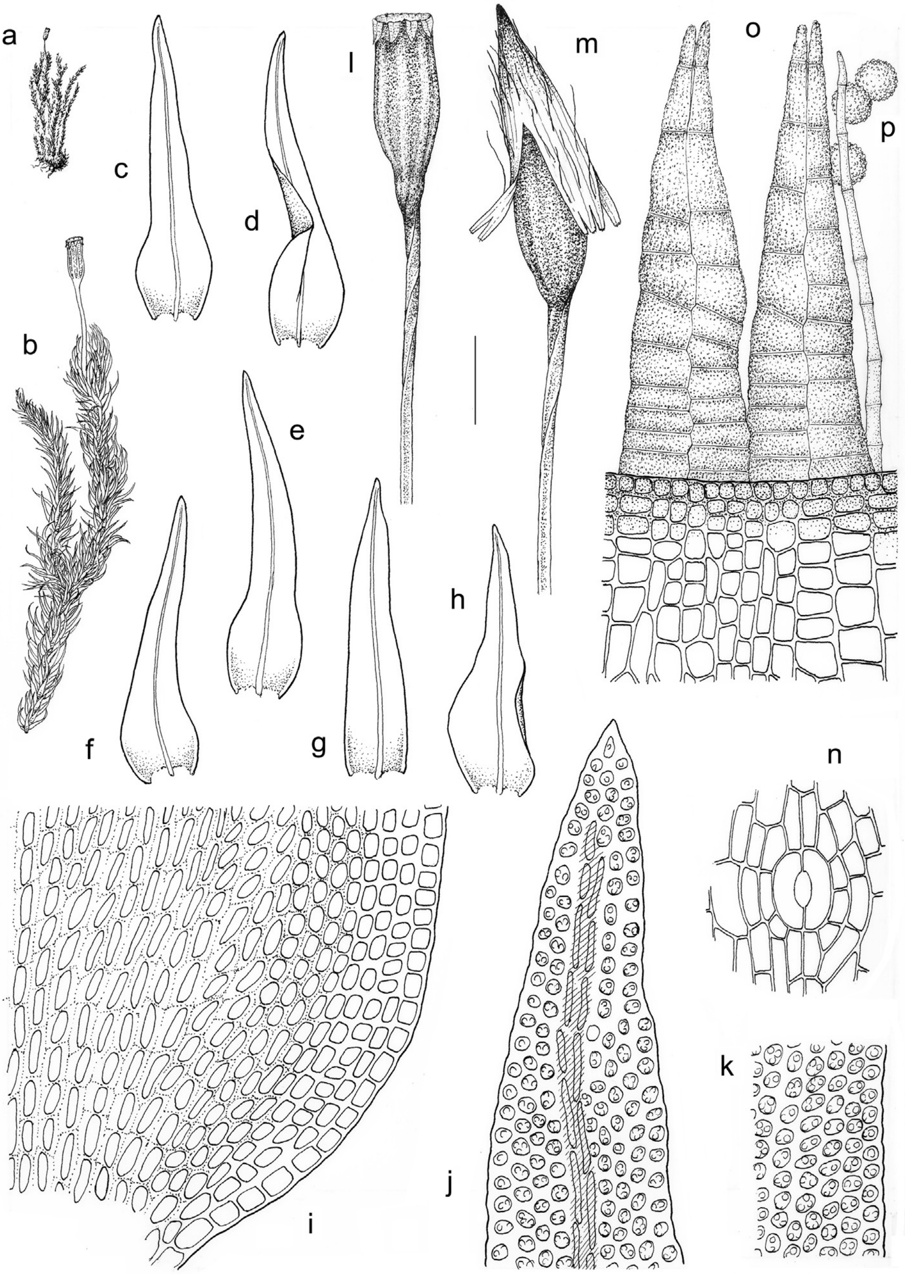


FIG. 154 – *Ulota reptans* Mitt. a–b. plant; c–f. leaves; g. outer perichaetial leaf; h. inner perichaetial leaf; i. basal marginal cells; j. top laminal cells; k. median marginal cells; l. an empty capsule in dry; m. a capsule with calyptra; n. stoma; o. a portion of peristome; p. spores. (Scale bar: a, 10 mm; b, 1.2 mm; c–h, l and m, 0.5 mm; i–k, 0.04 mm; n–p, 0.05 mm. All drawn from *Iwatsuki s.n.* [non-type, S] except g and h from *Iwatsuki s.n.*, 1955 [non-type, S]).

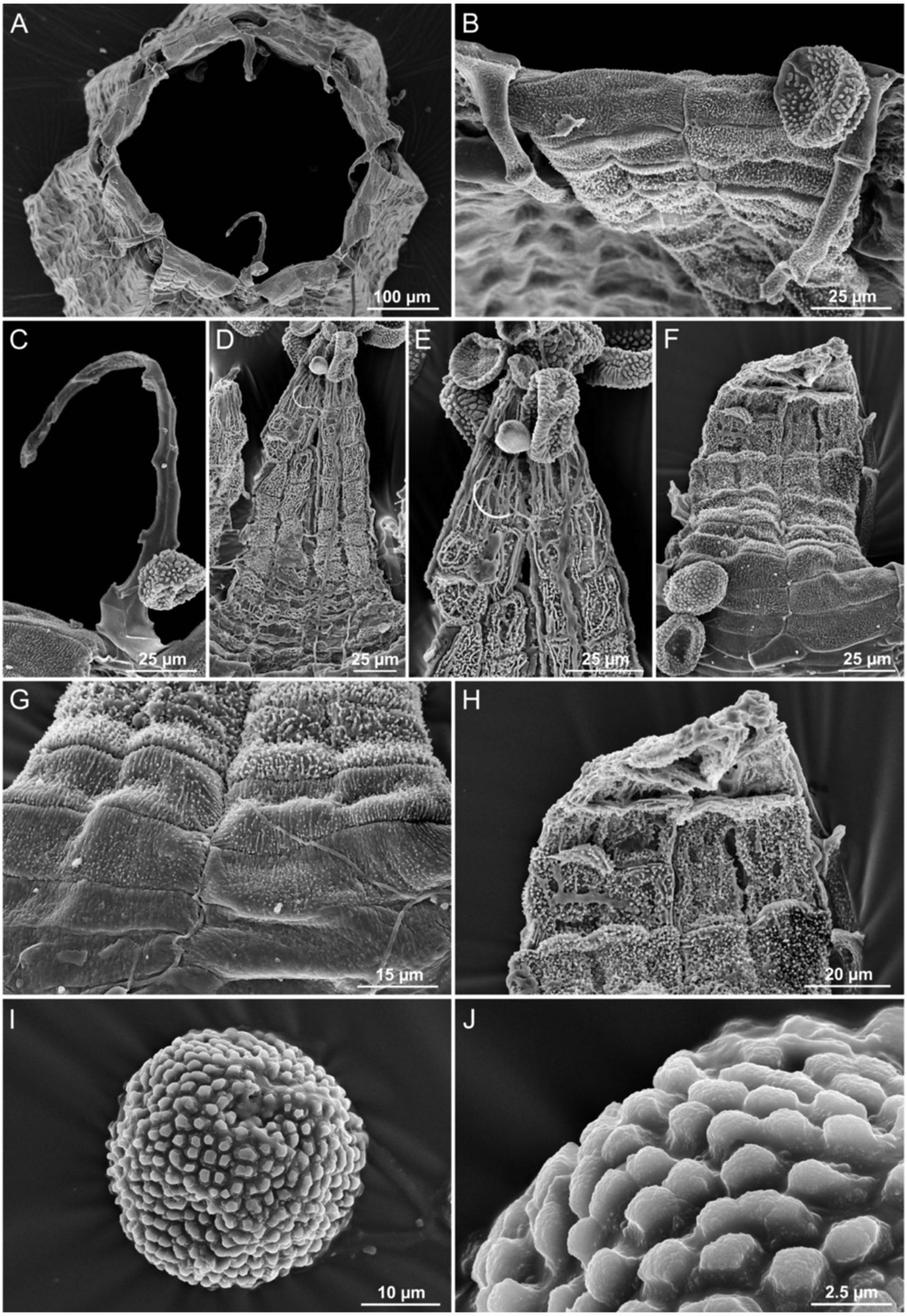


FIG. 155 – *Ulota reptans* Mitt. A, overview of peristome; B, inner view of basal peristome; C, outer surface of endostome; D, outer view of exostome; E, outer surface of upper exostome; F, inner view of exostome; G, inner surface of basal exostome; H, inner surface of upper exostome; I, a spore; J, surface ornamentation of a spore. (All from *Higuchi 41462* [non-type, TNS]).

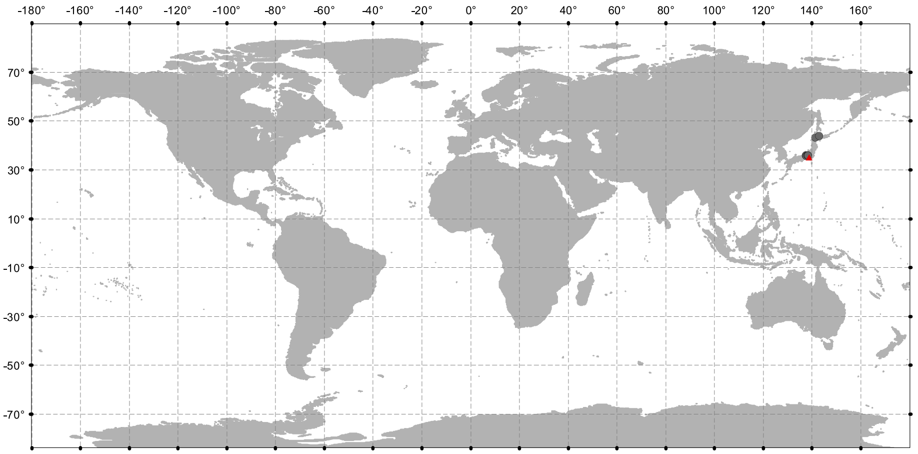


FIG. 156 – Distribution of *Ulota reptans* worldwide. The red triangle indicates the type locality.

long neck when dry, stomata located at the central part of capsules, longer seta (3–4.5 mm) and larger spores (41–51 μm).

Ulota reptans was also considered to have much in common with *U. rehmannii* (Fedosov and Ignatova, 2018; Wang and Jia, 2012a). In both, the leaves usually flexuose, capsules short-cylindrical and hardly constricted when dry, and endostome segments eight and narrow, but *Ulota rehmannii* differs in distinctly differentiated cells at basal leaf margins (3–6 rows), strongly variably striate exostome teeth and relatively small spores (28–32 μm).

No noteworthy variation within *Ulota reptans* was seen.

Key to *Ulota reptans* and its closely related species.

1. Spores multicellular, 87–105 μm; leaves variably crisped when dry.. *U. gigantospora*
1. Spores unicellular, 28–51 μm; leaves erect to flexuose when dry......................2
2. Leaves erect-appressed when dry; leaf cells at basal margins distinctly differentiated in 4–10 rows, with thin walls; capsules strongly constricted when dry; stomata often sporadically on the upper part of urn; calyptra always naked.. *U. macrocalycina*
2. Leaves erect to flexuose when dry; leaf cells at basal margins variably differentiated, with only thickened transverse walls; capsules hardly to moderately constricted when dry; stomata located at the base of urn or the junction between urn and neck; calyptra sparsely hairy, sometimes naked or moderately hairy...3
3. Capsules with long neck when dry; seta longer, 3–4.5 mm; spores large, 41–51 μm.. *U. megalospora*
3. Capsules with short neck when dry; seta relatively short, 2.5–3.3 mm; spores relatively small, 28–38 μm...4

4. Leaf cells at basal margins distinctly differentiated in 4–6 rows; exostome teeth prominently variably striate outside; spores small, 28–32 µm......... *U. rehmannii*
4. Leaf cells at basal margins weakly differentiated, no more than three rows; exostome teeth densely papillose outside; spores relatively large, 30–38 µm.. *U. reptans*

Additional Specimens Examined: **Japan**. Ishikawa: Mt. Hakusan, 22 Jul. 1982, *H. Akiyama 3141* (KYO). Nagano: Chino, 8 Aug. 1962, *S. Nakanishi s.n.* (HYO-C6-008265, 8266, 8267); Mt. Ontake, 25 Aug. 1953, *Z. Iwatsuki s.n.* (S); Mt. Yatsugatake, 4 May 1954, *Z. Iwatsuki s.n.* (S), 138°22′ E, 35°59′ N, 15 Oct. 2003, *M. Higuchi 41462* (TNS); Mt. Kisokoma, 26 Aug. 1955, *Z. Iwatsuki s.n.* (PC, S). Hokkaido: Kamikawa, 21 Aug. 1959, *S. Nakanishi 12335* (HYO), *12336* (HYO), *12343* (HYO), *12344* (HYO), 23 Aug. 1959, *12385* (HYO).

43. **Ulota rhytiore** (B.H. Allen) F. Lara, Garilleti, Albertos & Mazimpaka, Bryologist 111: 323. 2008. ≡ *Orthotrichum rhytiore* B.H. Allen, Monogr. Syst. Bot. Missouri Bot. Gard. 90: 639. f. 261. 2002. Type: El Salvador. Chalatenango, Mun. Ignacio, Cantón Río Chiquito, Cerro Pital, finca de los Sres. Portillo, cima de Cerro Pital, elev. 2730 m, 14°23′ N, 89°08′ W, exposed mountain top, disturbed low mossy forest, 21 Nov. 1993, *Sipman 37626A* (holotype, NY00799474!).

Plants ca. 1.6 cm tall, green on the top, brown to black below. Stems usually branched. Leaves flexuose, spiral, rarely crisped when dry, patent to spreading when moist, 4.2–5.1 mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded, concave; apex long acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells oblong, rounded, (11–) 13–17 (–22) × (7–) 9–10 (–11) µm, thick-walled, with low papillose; basal inner cells linear, elongate-rectangular, (28–) 32–46 (–56) × (6–) 7–8 (–9) µm, with thick wall, smooth; basal marginal cells often differentiated in 1–8 rows, hyaline, quadrate to rectangular, with transversely thickened walls.

Autoicous. Perichaetial leaves are somewhat longer, 5.2–5.4 mm. Vaginula not seen. Seta ca. 2 mm long. Capsule emergent. Urn fusiform, oblong-cylindrical or elliptical, puckered, ca. 2 mm long, yellow, strongly constricted at the mouth when dry, eight furrows only near the mouth. Neck short, gradually narrowed to the seta. Exothecial cells not seen. Stomata superficial, scattered throughout the urn. The peristome is apparently absent. Opercula with a long beak. Calyptra mitrate, with many hairs. Spores spherical, finely papillose, (25–) 29–33 (–37) µm in diameter.

Illustration: Albertos *et al.* (2008); figure 157.

Habitat: No phorophyte record is found in this study. There is only one altitudinal record is 2730 m.

Distribution: It is **endemic** to El Salvador. Figure 158.

Notes: *Ulota rhytiore* is the only species in Central America so far within *Ulota*, and all the available studies are based on scanty type material (Wang and Jia, 2016; Albertos *et al.*, 2008). In this case, we did not dissect any capsule from the holotype.

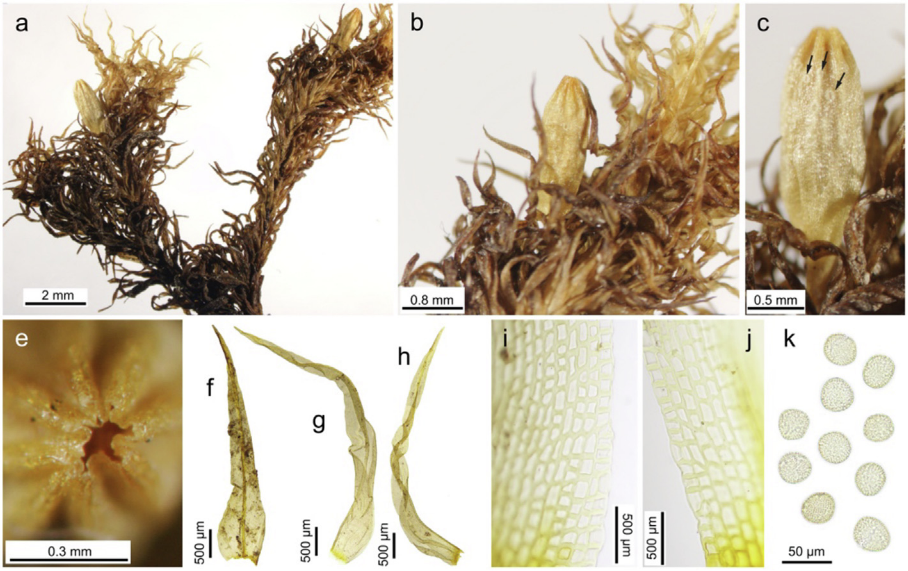


Fig. 157 – *Ulota rhytiore* (B.H. Allen) F. Lara, Garilleti, Albertos & Mazimpaka. a. Habit. b–c. Capsules in dry, with arrows indicating some stomata. e. Capsule mouth viewed from above. f. Leaf. g–h. Perichaetial leaves. i–j. Marginal cells at leaf base. k. Spores. (All from the holotype in NY).

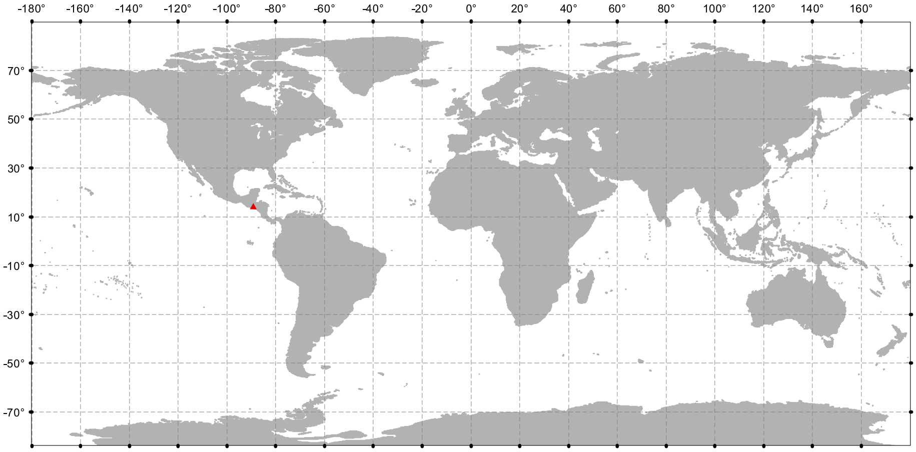


Fig. 158 – The type locality of *Ulota rhytiore.*

Ulota rhytiore is a very distinct species with elliptical capsules, puckered mouth, absent peristome, and stomata present throughout the urn. A Chinese species, *Ulota gymnostoma*, is very similar to *U. rhytiore* in capsule shape, lack of peristome and calyptra hairiness, but differs in the strongly crisped leaves, fully emergent to short exserted capsules and stomata located at the transition zone between urn and neck.

There is too scanty material to find any variation in *Ulota rhytiore*.

Key to *Ulota rhytiore* and its closely related species.

1. Capsules fully emergent to short exserted; stomata restricted to the base of urn or the junction of urn and neck; leaves strongly crisped when dry.. *U. gymnostoma*
1. Capsules emergent; stomata scattered throughout the urn; leaves strongly flexuose to spiral when dry.. *U. rhytiore*

Additional Specimens Examined: None.

44. **Ulota robusta** Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 49. 1859. Type: India. Sikkim. Himalaya orient. Reg. temp., *J. D. Hooker no.216* (lectotype, BM000852202! Designated by Guo *et al.*, 2010; isolectotype, NY), *219* (paralectotypes, NY, BM), *244* (paralectotypes, NY, BM).

Ulota bellissima Bescherelle, Annales des Sciences Naturelles; Botanique, sér. 7, 15 : 57. 1892. Type: China. Yunnan, on branches of trees, alt. 3000 m, 5 Aug. 1883, *Delavay 1647* (holotype, PC0083746! Isotypes, FI! S-B157798!). Proposed by Guo *et al.* (2010).

Plants 1–4 cm tall, green on the top and brown to black below. Stems usually branched. Leaves flexuose to moderately crisped when dry, patent to wide-spreading when moist, (2.2–) 3–3.7 (–3.9) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex long acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (5–) 8–12 (–16) × (5–) 9–12 (–15) μm, thick-walled, with low papillose; basal inner cells rhomboidal, elongate-rectangular or vermiculate, (21–) 32–45 (–64) × (1–) 2–4 (–7) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in (1–) 2–4 (–7) rows, hyaline, quadrate to rectangular, with transversely thickened walls.

Autoicous. Perichaetial leaves are somewhat longer, (2.8–) 3.7–4.3 (–4.8) mm. Vaginula naked. Seta (2–) 3–6 (–7) mm long, often twisted anticlockwise when dry. Capsule long exserted, 1.5–2 (–2.3) mm long. Urn subglobose to short-cylindrical, rarely cylindrical when moist, hardly constricted below the mouth when dry and empty, eight furrows almost along the entire length. Neck short, abruptly narrowed to the seta. Exothecial cells differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, reflexed when dry, often lying on the exothecium, lanceolate, densely papillose outside, papillose above and striate below inside. Endostome segments 8, lanceolate, sometimes united by some cells at the base, partially biseriate, 1/2–1/3 width of teeth in the middle, almost as tall as teeth, hyaline or yellowish, smooth outside, striate or slightly scabrous inside. Opercula with a short or medium-long beak. Calyptra mitrate, often very densely hairy. Spores spherical, finely papillose, (26–) 32–37 (–44) μm in diameter.

Illustration: Guo *et al.* (2010) and Wang and Jia (2012a); figures 159–161.

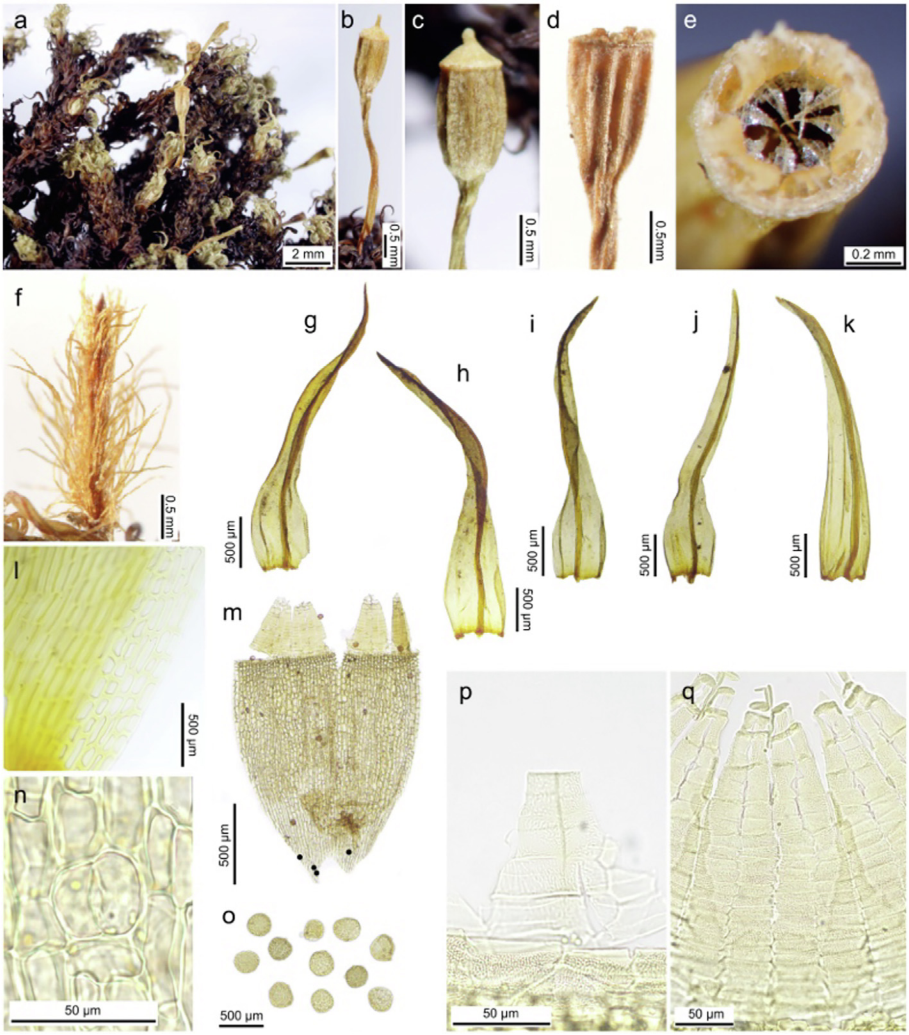


FIG. 159 – *Ulota robusta* Mitt. a. Habit. b–d. Capsules in dry. e. Capsule mouth viewed from above. f. Calyptra. g–j. Leaves. k. Inner perichaetial leaf. l. Marginal cells at leaf base. m. Exothecial wall, with dots indicating stoma position. n. Stoma. o. Spores. p. Endostome segments (broken). q. Exostome teeth. (a–c, e, m from *W.-Z. Ma 14-5694* [non-type, PE], d, f–l from *J. Kurz 2265* [non-type, H], n–q from *M.-Z. Wang 22311* [non-type, PE]).

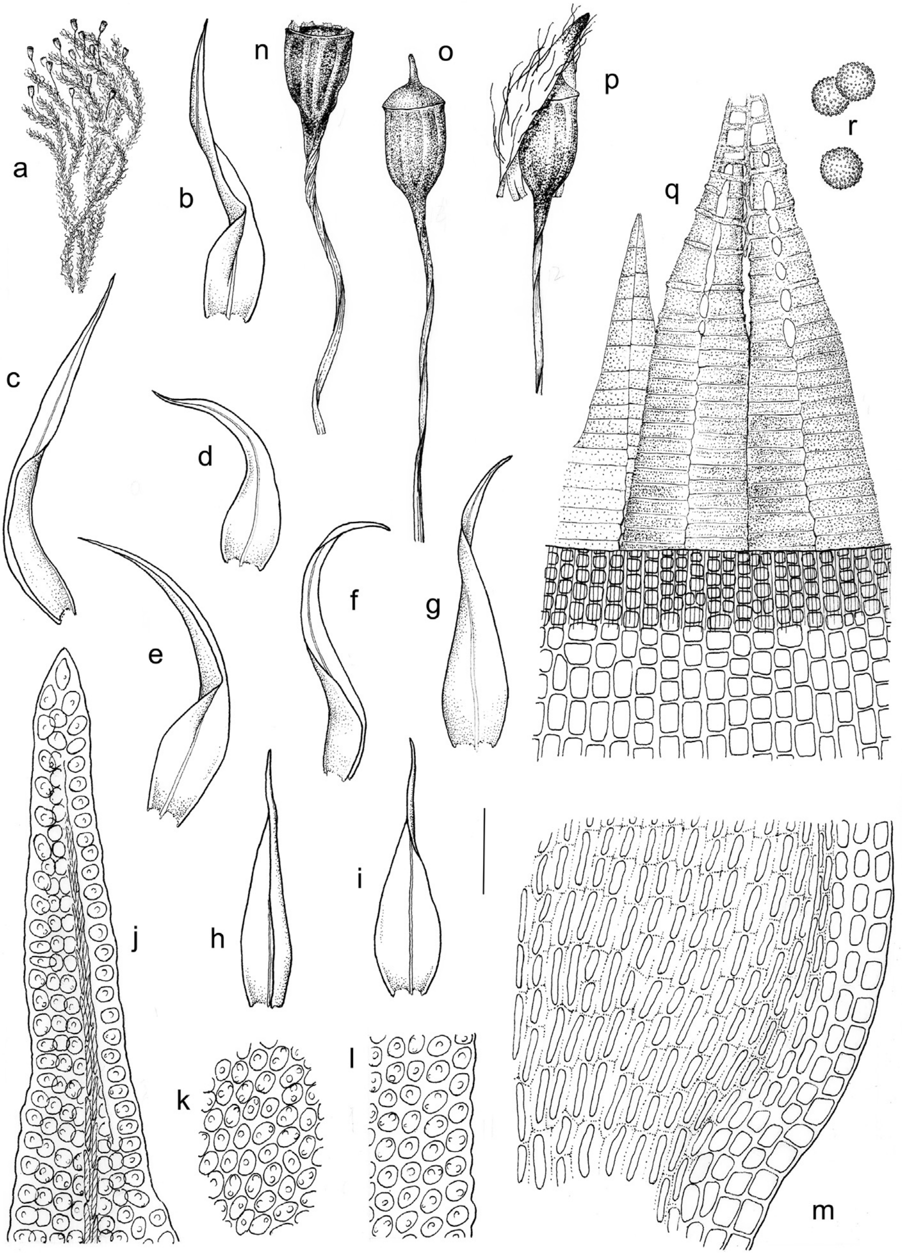


FIG. 160 – *Ulota robusta* Mitt. a. plant; b–g. leaves; h–i. inner perichaetial leaves; j. top laminal cells; k. median laminal cells; l. marginal laminal cells; m. basal marginal cells; n. an empty capsule in dry; o. a capsule with lid; p. a capsule with calyptra; q. a portion of peristome; r. spores. (Scale bar: a, 10 mm; b–i, o and p, 0.77 mm; j–m, 0.04 mm; n, 0.95 mm; q and r, 0.07 mm. a, h, i, o and p drawn from *Wang 83-837* [non-type, KUN], others from holotype of *U. bellissima* in FI).

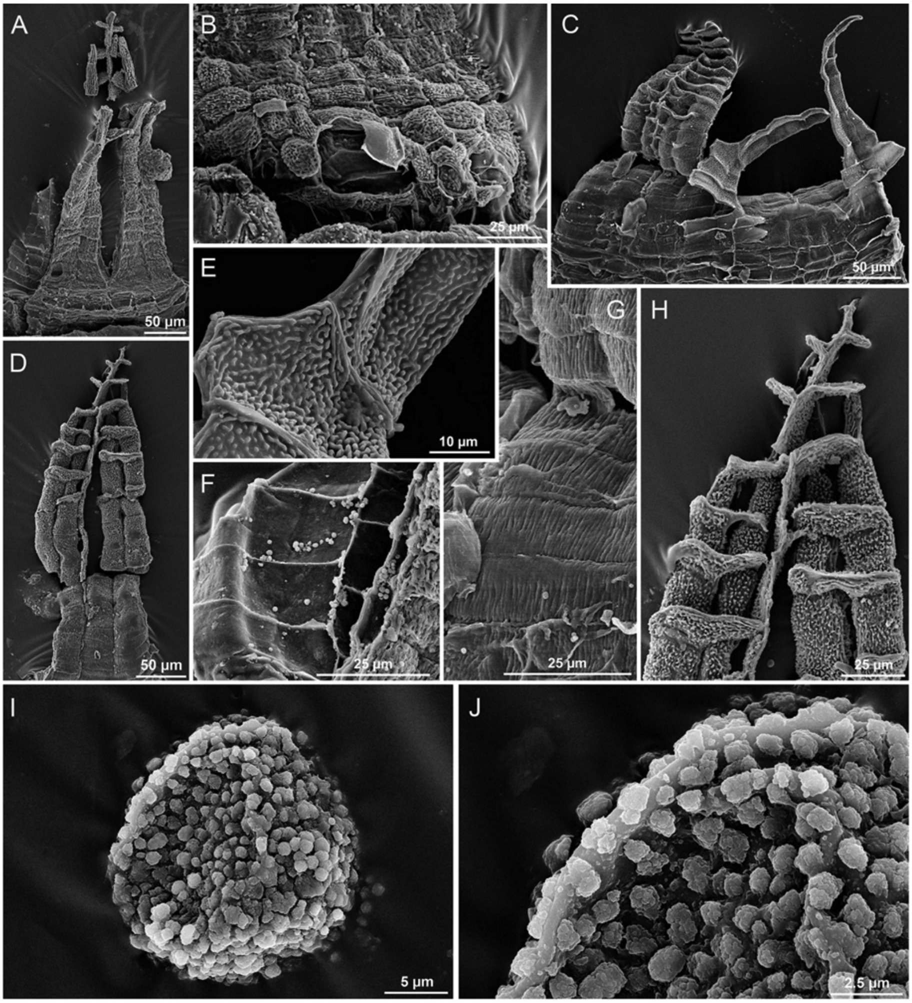


Fig. 161 – *Ulota robusta* Mitt. A, outer view of exostome; B, outer surface of basal exostome; C, inner view of peristome; D, inner view of exostome; E, inner surface of the middle part of endostome; F, outer surface of endostome; G, inner surface of basal exostome; H, inner surface of upper exostome; I, a spore; J, surface ornamentation of a spore. (All from the isotype of *U. bellissima* in S except A, D and H from *J. Kurz 2354* [non-type, S]).

Habitat: It grows on trunks and branches of trees or shrubs, such as *Cotoneaster*, *Pinus*, *Quercus*, and *Ribes*. There are many records of altitude: (2511–) 3050–3500 (–3987) m. It rarely occurs with *Orthotrichum hookeri* together.

Distribution: It is restricted to the Himalaya mountains, including Bhutan, China, Nepal, and India. Figure 162.

Notes: *Ulota robusta* is easily recognized by the flexuose to crisped leaves, often short-cylindrical capsule which is hardly constricted when dry, eight wide striate endostome segments, and calyptra often with very dense and long hairs.

At present, there are five species with wide endostome segments in the genus *Ulota* worldwide, *i.e. U. billbuckii*, *U. magellanica*, *U. latisegmenta*, *U. membranata*, and *U. robusta*. The first two species are from South America and they are different from *U. robusta* in flexuose leaves when dry, hardly differentiated (often <3 rows) leaf basal marginal cells, strongly constricted capsules, 16 endostome segments, and large spores (36–99 μm). The Australasian *Ulota membranata* is distinguished by erect to flexuose leaves, obovate to ovate-cylindrical capsules, 16 endostome segments and multicellular spores (84–105 μm). Finally, another Chinese species *Ulota latisegmenta* is most closely related to *U. robusta*, but differs in often strongly constricted capsules, finely papillose endostome segments, smaller plants (1–2 cm), and smaller spores (19–25 μm).

There are some variations in leaf crispness, capsule shape, contraction degree of capsule, and calyptra hairiness in *Ulota robusta*. For example, materials from Yunnan Province often have short-cylindrical capsules, while those from Sichuan Province mostly have cylindrical capsules. These variations result in the previous delimitation between *Ulota robusta* and *U. latisegmenta* being not so clear. Therefore, some of the Sichuan materials are difficult to determine which species they belong to, and we thus did not list them here. Finally, these problems need further study in the future.

Key to *Ulota robusta* and its closely related species.

1. Spores multicellular, 84–105 μm..2
1. Spores unicellular, 19–44 μm..3
2. Capsules obovate to ovate-cylindrical; leaf cells at basal margins distinctly differentiated, 4–6 rows; endostome segments almost free at bases........ ....*U. membranata*
2. Capsules cylindrical; leaf cells at basal margins hardly differentiated, often one row; endostome segments united by some irregularly shaped cells at the lower half part..*U. billbuckii*
3. Leaves erect, sinuose and falcate when dry; capsules calyptra sparsely hairy to naked; spores large, 36–44 μm..*U. magellanica*
3. Leaves flexuose to crisped when dry; calyptra densely hairy; spores small, 19–37 μm..4
4. Endostome segments 16, finely papillose; capsules short- to long-cylindrical; leaves moderately to strongly crisped when dry; plants smaller, 1–2 cm; spores smaller, 19–25 μm..*U. latisegmenta*
4. Endostome segments 8, striate; capsules subglobose to short-cylindrical; leaves flexuose to moderately crisped when dry; plants larger, 1–4 cm; spores larger, 32–37 μm..*U. robusta*

Additional Specimens Examined: **Bhutan**. SANNK: s. loc., *Griffith 145* (H, MICH).

China. CHONGQING: Jinfoshan, Aug. 1945, *C. C. Gao K. F. 61* (PE). SICHUAN (=SETSCHWAN): Emei Mt., 11 Aug. 1937, *L.-Y. Dai 205* (PE), 11 Aug. 1939, *T206*

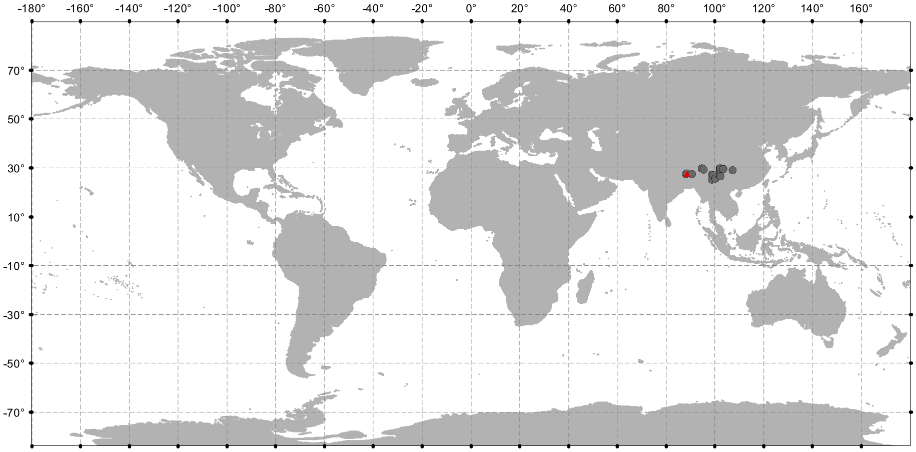


FIG. 162 – Distribution of *Ulota robusta* worldwide. The red triangle indicates the type locality.

(PE), 1939, *T117* (PE), 25 Aug. 1942, *P.-C. Chen 5619a* (PE), *5619c* (PE), 2 Jul. 1957, *L.-Z. Hu 57-84* (PE), 2 Aug. 1980, *Q. Li 5181* (IFP), *5183* (IFP), *Q. Gao et al. 18837* (IFP); Huili Co., Mt. Lungdschu-schan, 25 Mar. 1914, *Handel-Mazzetti 24* (S), *996* (S), *s.n.* (E); Luding Co., Hailuogou, 9 Oct. 2021, *Z.-Q. Yi Q271* (PE), 10 Oct. 2021, *Q313* (PE), Yanzigou, 13 Oct. 2021, *Z.-Q. Yi Q511* (PE); Mabian Co., Dafengding Nature Reserve, 7 Jul. 2012, *Q. He H5330* (PE); Mianning Co., Yele Nature Reserve, 28°56.283′ N, 102°06.268′ E, 9 Jul. 2005, *Jia 08198* (PE); Miyi Co., Malong, 7 Jul. 1983, *L.-S. Wang 83-540* (KUN, PE), *K.-K. Chen 285* (PE), *310* (PE), *M.-Z. Wang 21075-a* (PE); Tianquan Co., Erlangshan, 21 Jul. 1980, *Q. Gao 17690* (IFP, PE); Yanyuan Co., 26 Jul. 1983, *L.-S. Wang 83-837* (KUN, PE), 9 Aug. 1983, *83-924* (KUN). XIZANG: Linzhi, Bayi, 3 Aug. 2017, *s.coll.* (PE); Motuo Co., 29 Apr. 1983, *Y.-G. Su 4463* (PE). YUNNAN: Baoshan, Tengchong, 8 Jul. 2014, *W.-Z. Ma 14-5694* (PE); Dali Co., 100°06′ E, 25°40′ N, 20 Sep. 2006, *Blanka Shaw 5632* (DUKE), Cangshan, 15 Jun. 2010, *W.-Z. Ma 10-1141* (KUN), 15 Jul. 2010, *10-1151* (PE), 8 Aug. 2010, *s.n.* (PE); Fugong Co., 7 May 2004, *J. R. Shevock 25558* (E); Weixi Co., Weideng, 23 May 1982, *M.-Z. Wang 6281* (PE), 24 May 1982, *6352-b* (PE), *6354* (PE), *L.-S. Wang 353* (PE);

India. SIKKIM: Phalut, 18 Oct. 1868, *J. Kurz 2265* (BM, H); Phaccost, s. date, *2354* (S); s. loc., s. date, *J. Kurz s.n.* (S).

Nepal. TAPLEJUNG: Milke Danda ridge, 23 Oct. 1991, *D. G. Long s.n.* (E).

45. **ULOTA RUBELLA** E.B. Bartram, Lloydia 5: 269. 26. 1942. TYPE: PAPUA NEW GUINEA. Mt. Wilhemina, epiphyte, subalpine forest, E. Wilhelmina-top, alt. 3700 m, 24 Sep. 1938, *L. J. Brass & E. Myer-Drees no. 10374* (holotype, FH00079858–59! isotypes, L.0060832! MICH526543!).

Plants 1–2 cm tall, yellow to green above, brown to dark brown below. Stems usually branched. Leaves strongly crisped when dry, wide-spreading to patent when moist, (2.3–) 2.7–2.9 (–3.1) mm long, leaf lamina narrow lanceolate, unistratose; leaf base wide, ovate, distinctly concave; apex long acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells oblong, rounded, (8–) 10–14 (–19) × (3–) 4–7 (–10) μm, thick-walled, often with two low simple papillae per cell; basal inner cells linear, rectangular, elongate-rectangular to vermicular, (15–) 31–45 (–59) × 2–5 (–8) μm, with strongly thickened wall, smooth; basal marginal cells weakly differentiated, 1–2 rows, hyaline, quadrate to rectangular, with transversely thickened walls.

Autoicous. Perichaetial leaves somewhat longer, (2.8–) 3–3.5 (–3.9) mm. Vaginula not seen. Seta (6.2–) 6.5–10 (–10.5) mm long, twisted anticlockwise when dry. Capsule long exserted, 1.8–2.5 mm long. Urn cylindrical strongly constricted below the mouth when dry and empty, with eight furrows along the entire length, with prominent ribs alternately. Neck short, gradually narrowed to the seta. Exothecial cells differentiated into eight bands, almost as long as an urn, usually four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, on the transition zone between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry and lying on the exothecium, lanceolate, densely papillose on the outside, striate above and nearly smooth below on the inside. Endostome segments 8, linear-lanceolate, 2/3 to almost reaching the exostome teeth, uniseriate upper, irregularly biseriate at the base, hyaline, variably incurved when dry, smooth on both sides. Opercula not seen. Calyptra mitrate, sparsely hairy. Spores spherical, finely papillose, (29–) 35–39 (–44) μm in diameter.

Illustration: Vitt *et al.* (1993); figures 163–165.

Habitat: It grows on trees, but no phorophyte was recorded. There is only one record of altitude: ca. 3700 m. No mixed growth has been found in this study.

Distribution: It is **endemic** to Papua New Guinea. Figure 166.

Notes: *Ulota rubella* is recognized by a combination of characters, including strongly crisped leaves, hardly differentiated cells at basal leaf margins, quite a long seta, strongly constricted cylindrical capsules, narrow endostome segments, and sparsely hairy calyptra.

Ulota rubella is similar to the local species *U. splendida*, both having strongly crisped leaves, hardly differentiated cells at basal leaf margins, very long seta, and strongly constricted cylindrical capsules. However, *Ulota splendida* differs in larger plant (2–3 cm), slightly sparse arrangement of leaves on stems and branches, longer capsules (2–3.2 mm), slightly rough endostome segments, and densely hairy calyptra. Moreover, *Ulota rubella* also resembles another local species, *U. angusti-limbata*, they share the same characteristics as those between *U. rubella* and *U. splendida*. But *Ulota angusti-limbata* is distinguished by the short-cylindrical capsules that are more or less constricted when dry, shorter leaves (2.2–2.4 mm), and densely hairy calyptra.

We have never found any non-type specimens of *Ulota rubella* so far, and thus no obvious variation was observed.

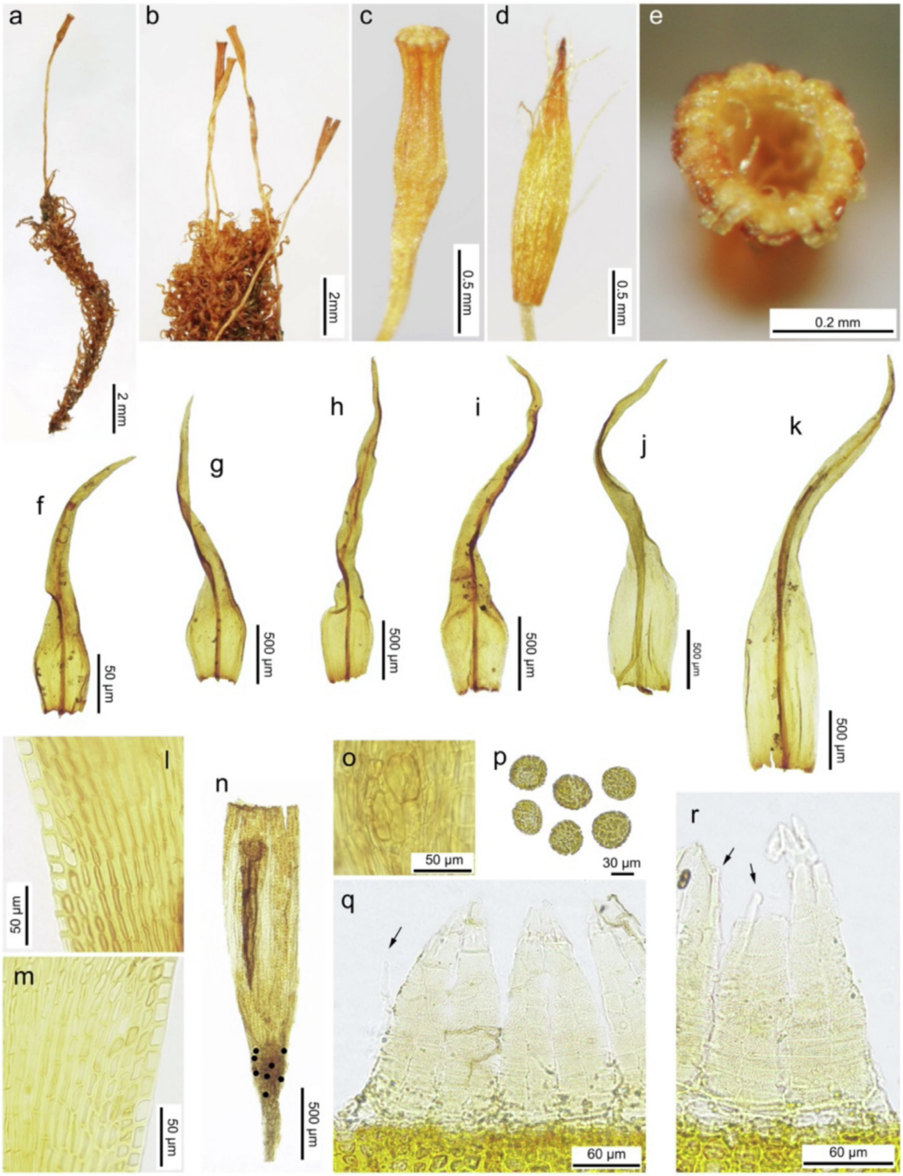


Fig. 163 – *Ulota rubella* E.B. Bartram. a–b. Habit. c. A capsule in dry and empty. d. Calyptra. e. Capsule mouth viewed from above. f–i. Leaves. j–k. Perichaetial leaves. l–m. Marginal cells at leaf base. n. Exothecial wall, with dots indicating stoma position. o. Stomata. p. Spores. q–r. Peristome with arrows indicated endostome segments. (All from the holotype in FH).

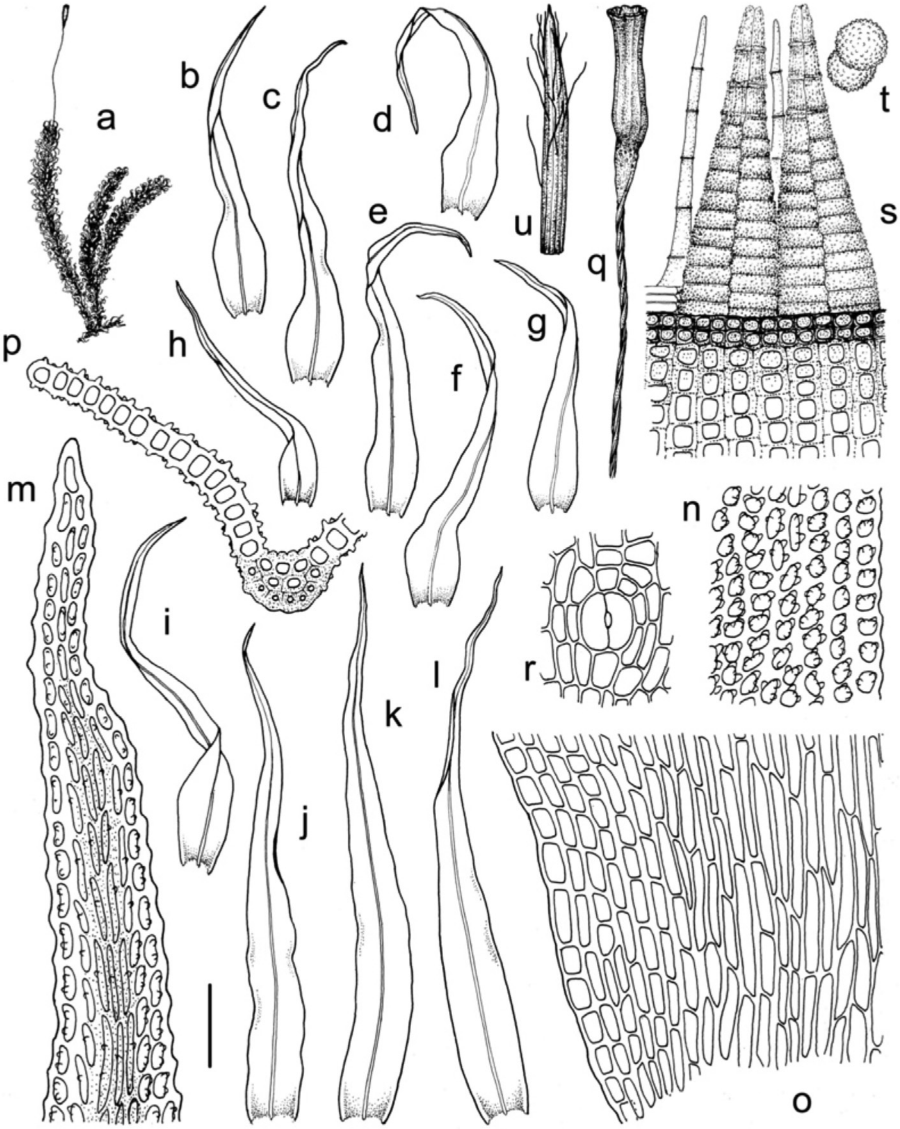


FIG. 164 – *Ulota rubella* E.B. Bartram. a. plant; b–i. leaves; j–l. perichaetial leaves; m. top laminal cells; n. marginal laminal cells; o. basal marginal cells; p. partial cross section of leaf; q. an empty capsule in dry; r. stoma; s. a portion of peristome; t. spores; u. calyptra. (Scale bar: a, 5 mm; b–l, 0.77 mm; m–p, 0.04 mm; q and u, 1.0 mm; r–t, 0.05 mm. All drawn from holotype in FH).

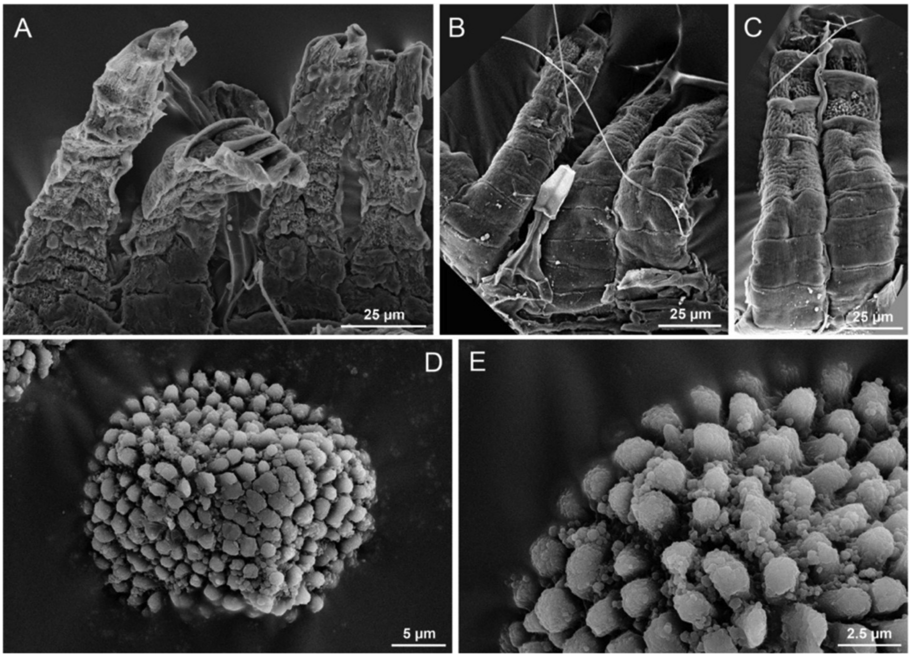


Fig. 165 – *Ulota rubella* E.B. Bartram. A, outer view of exostome; B, inner surface of peristome; C, inner surface of exostome; D, a spore; G, surface ornamentation of a spore. (All from the holotype in FH).

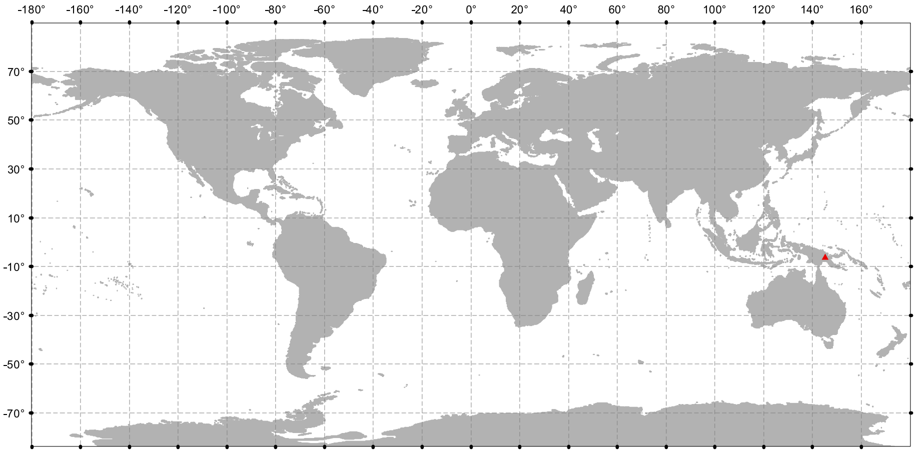


Fig. 166 – The type locality of *Ulota rubella*.

Key to *Ulota rubella* and its closely related species.

1. Plant large, 2–3 cm; capsules long-cylindrical, 2–3.2 mm; endostome segments slightly coarse; leaves arranged relatively sparsely on stems and branches.. *U. splendida*
1. Plant relatively small, 0.5–2 cm; capsules short-cylindrical to cylindrical, 1–2.5 mm; endostome segments smooth; leaves arranged densely on stems and branches..2
2. Capsules short-cylindrical, more or less constricted when dry; leaves shorter, 2.2–2.4 mm; calyptra densely hairy...................................... *U. angusti-limbata*
2. Capsules cylindrical, strongly constricted when dry; leaves longer, 2.7–2.9 mm; calyptra sparsely hairy... *U. rubella*

Additional Specimens Examined: None.

46. **ULOTA SPLENDIDA** E.B. Bartram, Lloydia 5: 269. 27. 1942. TYPE: PAPUA NEW GUINEA. Mt. Wilhemina, abundant as an epiphyte in subalpine forest, 2 km. E. of Wilhemina-top, alt. 3800 m., Sep. 1938, *L. J. Brass & E. Myer-Drees no. 10137* (holotype, FH00079860–61! isotypes, BM000844913! L0060833! MICH!).

Ulota hattorii Iwatsuki, J. Hattori Bot. Lab. 32: 280. f. 7. 1969. TYPE: MALAYSIA [BORNEO]. Sabah: Mt. Kinabalu. On branches and trunks of trees, on granodiorite slope below Sayat Sayat, alt. 3350–3700 m, 20 May 1963, *Z. Iwatsuki 949* (holotype, NICH250949!). Porposed by Wang and Jia (2012a).

Plants (1–) 2–3 (–9) cm tall, yellow to green on the top, brown to dark brown below. Stems usually branched. Leaves strongly crisped, sometimes flexuose when dry, erect-spreading to patent when moist, (2.5–) 2.8–3.3 (–3.9) mm long; leaf lamina narrow lanceolate, unistratose; leaf base slightly wide, ovate; apex long acuminate, often tortuose or flexuose; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells oblong or rounded, (5–) 9–12 (–15) × (5–) 6–8 (–10) μm, thick-walled, with low papillose; basal inner cells rhombic, elongate-rectangular and vermiculate, (29–) 34–56 (–83) × (1–) 2–4 (–5) μm, with strongly thickened wall, smooth; basal marginal cells weakly differentiated, 1–2 rows, rarely up to 4 rows, hyaline, quadrate to rectangular, with transversely thickened walls.

Autoicous. Perichaetial leaves somewhat longer, (3.9–) 4.1–4.8 (–5.6) mm. Vaginula not seen. Seta 7–8 mm long, twisted anticlockwise when dry. Capsule long exserted, 2–3.2 (–3.4) mm long. Urn long cylindrical when dry and empty, strongly constricted below the mouth when dry and empty, and eight furrows almost along the entire length. Neck short or slightly long, abruptly or gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, usually four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, reflexed when dry, lanceolate, densely papillose outside, striate inside. Endostome segments 8, narrow-lanceolate, as tall as teeth, biseriate, sometimes uniseriate at the upper part, ca. 1/3 width of teeth in the middle, hyaline or yellowish, smooth outside, slightly coarse inside. Opercula with a long beak. Calyptra mitrate, densely, rarely sparsely hairy. Spores spherical, finely papillose, (25–) 29–33 (–40) μm in diameter.

Illustration: Iwatsuki (1969), Vitt *et al.* (1993) and Wang and Jia (2012a); figures 167–169.

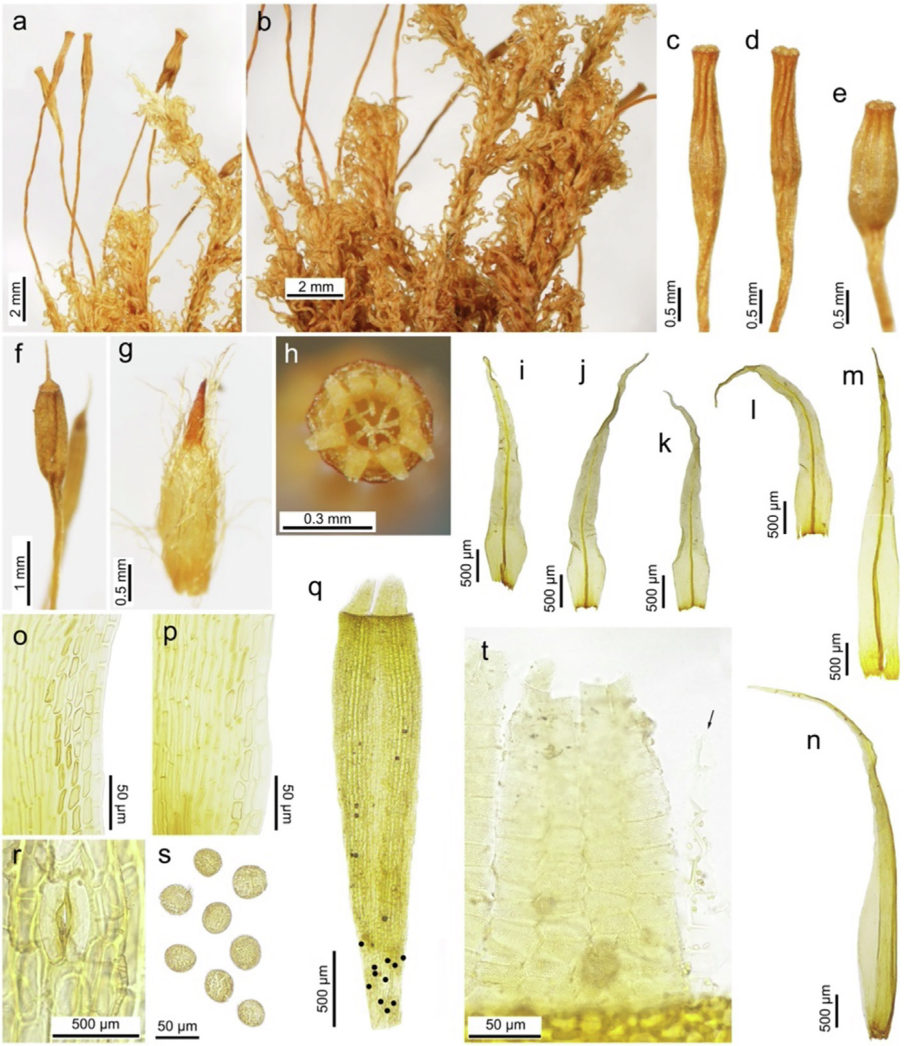


Fig. 167 – *Ulota splendida* E.B. Bartram. a–b. Habit. c–f. Capsules in dry. g. Calyptra. h. Capsule mouth viewed from above. i–l. Leaves. m–n. Perichaetial leaves. o–p. Marginal cells at leaf base. q. Exothecial wall, with dots indicating stoma position. r. Stoma. s. Spores. t. Peristome with an arrow indicating endostome segment. (All from the holotype in FH except s from *T. Koponen 32460* [non-type, S]).

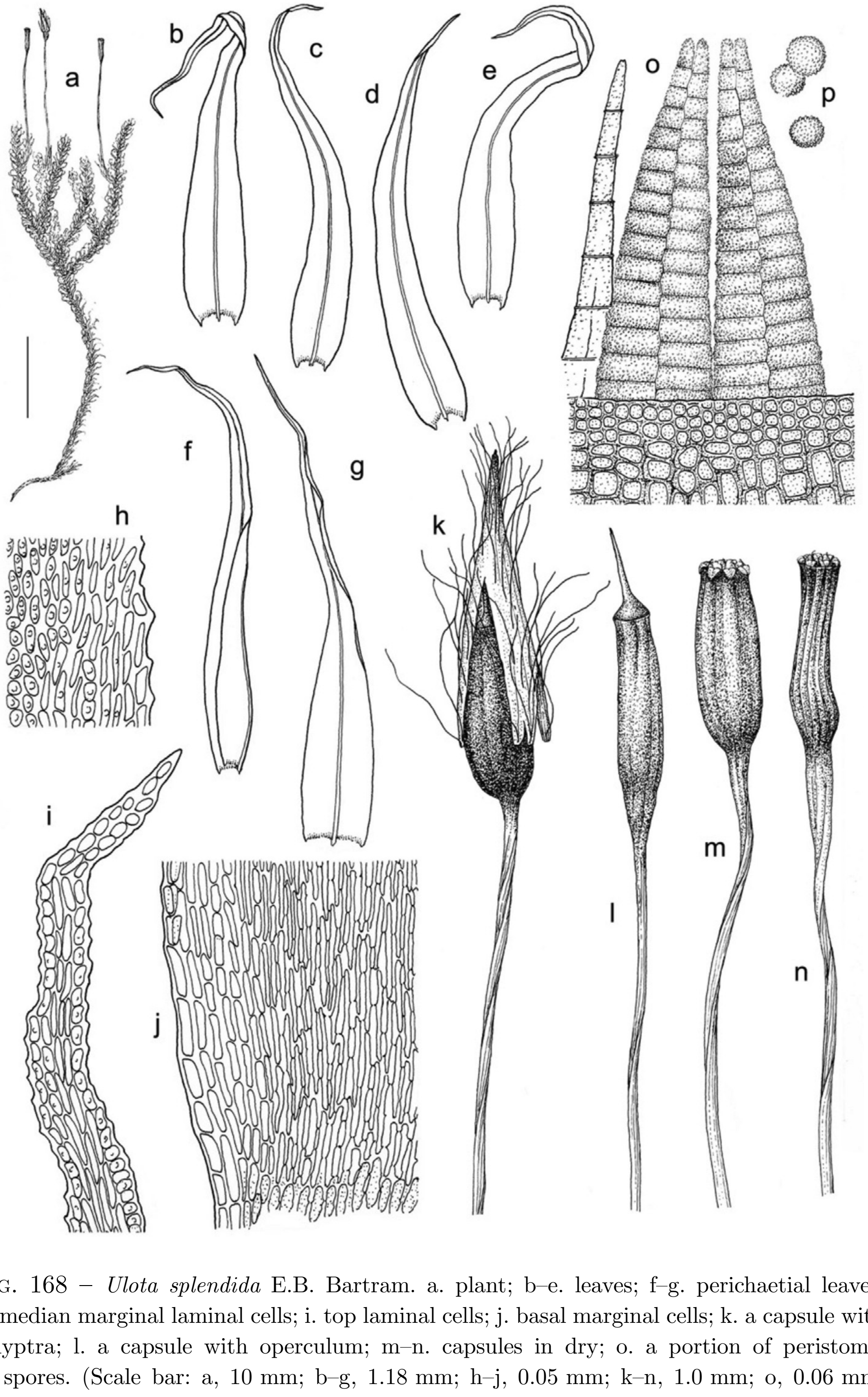


FIG. 168 – *Ulota splendida* E.B. Bartram. a. plant; b–e. leaves; f–g. perichaetial leaves; h. median marginal laminal cells; i. top laminal cells; j. basal marginal cells; k. a capsule with calyptra; l. a capsule with operculum; m–n. capsules in dry; o. a portion of peristome; p. spores. (Scale bar: a, 10 mm; b–g, 1.18 mm; h–j, 0.05 mm; k–n, 1.0 mm; o, 0.06 mm; p, 0.1 mm. All drawn from holotype in FH).

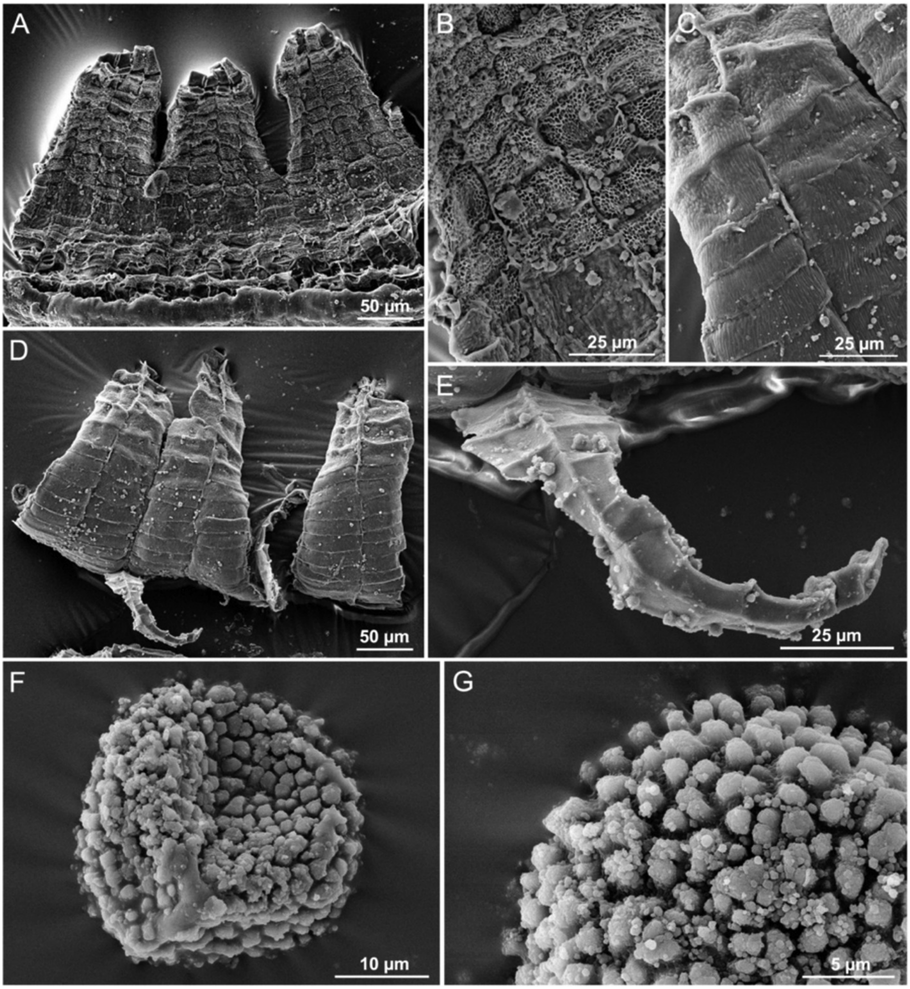


Fig. 169 – *Ulota splendida* E.B. Bartram. A, outer view of exostome; B, outer surface of lower exostome; C, inner surface of lower exostome; D, inner view of peristome; E, outer surface of endostome; F, a spore; G, surface ornamentation of a spore. (All from the holotype in FH).

Habitat: It grows on branches and trunks of trees and shrubs, such as *Rhododendron*. There are some records of altitude: 3300–3800 m. No mixed growth has been found in this study.

Distribution: It occurs in Papua New Guinea and Malaysia. Figure 170.

Notes: *Ulota splendida* is almost the largest species in *Ulota*, of which the plants can be high up to 9 cm. Besides that, its diagnostic characteristics also include weakly differentiated cells at basal leaf margins, long cylindrical capsules, quite a long seta, eight endostome segments, and densely hairy calyptra.

Only a few species in *Ulota* worldwide have such large plant size and very long seta. Among them, *Ulota obtusiuscula* from North America is the most similar to

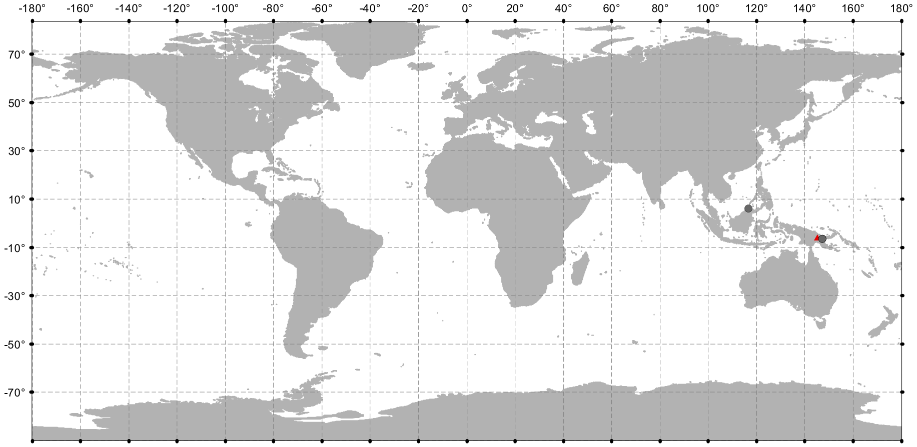


FIG. 170 – Distribution of *Ulota splendida* worldwide. The red triangle indicates the type locality. The dot in Malaysia is based on the type locality of *U. hattorii*.

U. splendida. Besides the above, they also share in the strongly crisped leaves, eight narrow-lanceolate endostome segments, and densely hairy calyptra. However, *Ulota obtusiuscula* differs in the more rows of hyaline cells at basal leaf margins (3–7 rows), shorter capsules (1.3–2 mm) with a long neck, and hardly or slightly constricted when dry.

Actually, *Ulota splendida* is the most similar to the local species *U. rubella*, both having strongly crisped leaves, hardly differentiated cells at basal leaf margins, very long seta, and strongly constricted cylindrical capsules. But *Ulota rubella* differs in the smaller plant (1–2 cm), densely arrangement of leaves on stems and branches, relatively short capsules (1.8–2.5 mm), smooth endostome segments, and sparsely hairy calyptra.

The plant size in *Ulota splendida* varies greatly, with mostly ranging from 2 cm to 3 cm and few up to 9 cm based on our observation.

Key to *Ulota splendida* and its closely related species.

1. Leaf basal marginal cells differentiated in more rows (3–7); capsules with long neck, hardly or slightly constricted when dry; seta relatively short, 5–7.5 mm.......... *U. obtusiuscula*
1. Leaf basal marginal cells hardly differentiated, often only 1–2 rows; capsules with short neck, strongly constricted when dry; seta quite long, 6.5–10 mm.......... 2
2. Plant small, 1–2 cm; capsules relatively short, 1.8–2.5 mm; endostome segments narrow (linear-lanceolate) and smooth; calyptra sparsely hairy; leaves arranged densely on stems and branches.......... *U. rubella*
2. Plant large, 2–3 cm; capsules long, 2–3.2 mm; endostome segments little wider (narrow-lanceolate) and slightly coarse; calyptra densely hairy; leaves arranged relatively sparsely on stems and branches.......... *U. splendida*

Additional Specimens Examined: **Papua New Guinea**. Morobe: Mt. Sarawaket Southern Range, 2.5 km S of Lake Gwam, 147°07′ E, 6°21′ S, 9 Jul. 1981, *T. Koponen 32595* (H), *32625* (H), *32651* (H), *32728* (H), *D. H. Norris 63192* (H), *63236* (H), *63298* (H), 3 km E of Lake Gwam, 147°09′ E, 6°19.5′ S, 8 Jul. 1981, *T. Koponen 32356* (H), *32361* (H), *32365* (H), *32443* (H), *32460* (S), 3 km S of Lake Gwam, 8–9 Jul. 1981, *D. H. Norris 62960* (H), *63030* (H), *63139* (H), *63314* (H), *63316* (H), *63318* (H), *63319* (H), 4 km E of Lake Gwam, *D. H. Norris 62565* (H), *T. Koponen 31794* (H), *31795* (H), *31797* (H), *32471* (H), 5 km E of Lake Gwam, 8 Jul. 1981, *T. Koponen 32493* (H), 6 km E of Lake Gwam, *T. Koponen 32521* (H).

47. **Ulota streptodon** Garilleti, Mazimpaka & F. Lara, Bryologist 115: 594. 2012. Type: Chile. Región de Magallanes Y de La Antártica Chilena. Provincia Antártica Chilena. Comuna de Cabo de Hornos. Parque Nacional Alberto de Agostini, south-central coast of Isla Gordon, Caleta Caracoles, NW of Estero Fouqué along SW arm of Beagle Channel, 55°01′ 57″ S, 69°36′41″ W, 5 m a.s.l., patches of tundra and disperse small areas of shrubby *Nothofagus betuloides*, horizontal branches of *Nothofagus betuloides* close to the shoreline, 20 Jan. 2012, *R. Garilleti s.n.* (holotype, NY; isotype, VAL).

Plants 0.5–1.5 cm tall, green above, yellow to brown below. Stems usually branched. Leaves erect, sinuose to flexuose when dry, erect-spreading when moist, (1.6–) 1.9–2.2 (–2.3) mm long; leaf lamina narrow lanceolate, unistratose; leaf base wide, long ovate; apex long acuminate, often sinuose; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells rounded, rarely oblong, (5–) 7–10 (–11) × (4–) 6–7 (–9) μm, thick-walled, with low papillose; basal inner cells linear, rectangular, elongate-rectangular, (19–) 23–44 (–55) × (1–) 2 (–3) μm, with thick wall, smooth; basal marginal cells weakly differentiated, often only one row, hyaline, quadrate to rectangular, with longitudinal and transversal walls slightly, equally thickened.

Autoicous. Perichaetial leaves somewhat longer, (2.1–) 2.2–2.7 (–2.8) mm. Vaginula is densely hairy. Seta ca. 3 mm long, often twisted anticlockwise when dry. Capsule short to long exserted, ca. 1.4 mm long. Urn cylindrical when dry and empty, moderately constricted below the mouth when dry and empty, somewhat puckered at the mouth, eight furrows almost along the entire length. Neck short or slightly long, gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, four to five cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, scattered on the urn. Preperistome not seen. Peristome single. Exostome teeth 16, often united into 8 pairs, variably erect or spreading to reflexed when dry, rarely lying on the exothecium, lanceolate, densely and finely papillose on both sides. Endostome segments are absent or sometimes rudimentary. Opercula not seen. Calyptra mitrate, densely hairy. Spores irregularly shaped, finely papillose, (91–) 109–126 (–134) μm in diameter, multicellular.

Illustration: Garilleti *et al.* (2012); figure 171.

Habitat: It grows on trunks and branches of trees (Garilleti *et al.*, 2012), such as *Nothofagus*. There are only two records of altitude in this study: 5–305 m. No mixed growth has been found in this study.

Distribution: It is **endemic** to the southern part of Chile. Figure 172.

Notes: *Ulota streptodon* is easily distinguished by the giant multicellular spores, erect to sinuose leaves, only 1–2 rows of hyaline basal marginal leaf cells, puckered capsule mouth, and absent endostome segments.

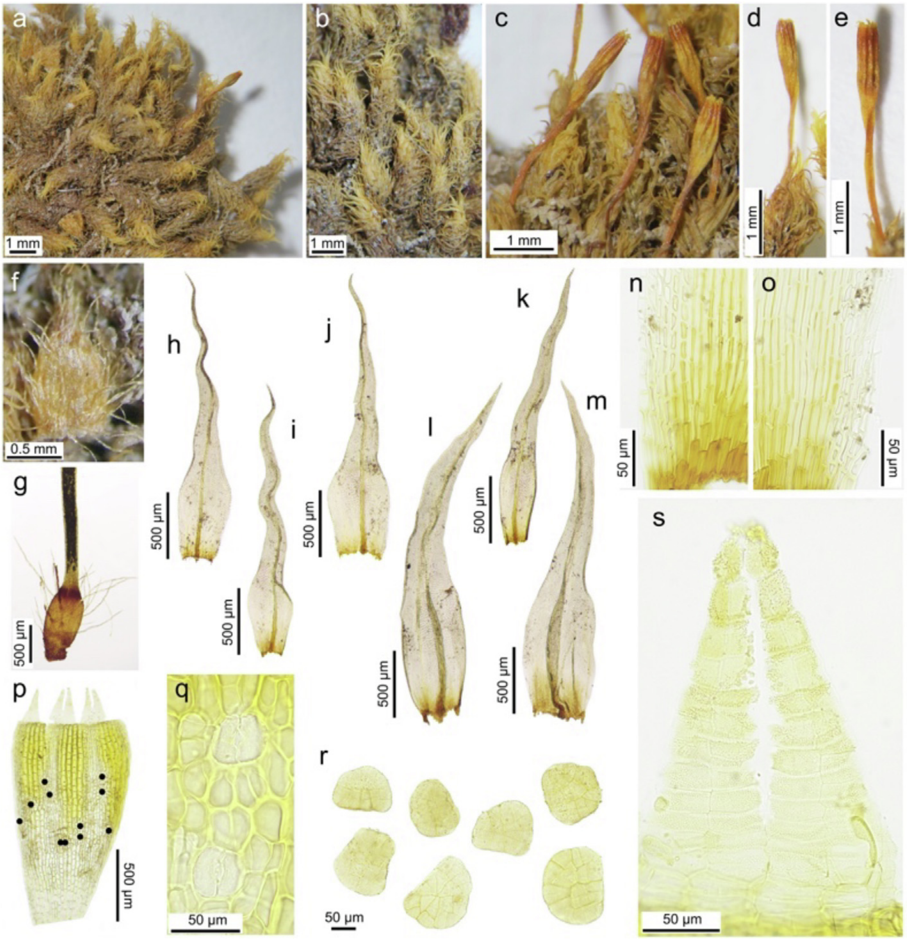


FIG. 171 – *Ulota streptodon* Garilleti, Mazimpaka & F. Lara. a–b. Habit. c–e. Capsules in dry and empty. f. Calyptra. g. Vaginula. h–k. Leaves. l–m. Perichaetial leaves. n–o. Marginal cells at leaf base. p. Exothecial wall, with dots indicating stoma position. q. Stomata. r. Spores. s. Peristome. (All from *A. Hollermager 1668* [non-type, PC]).

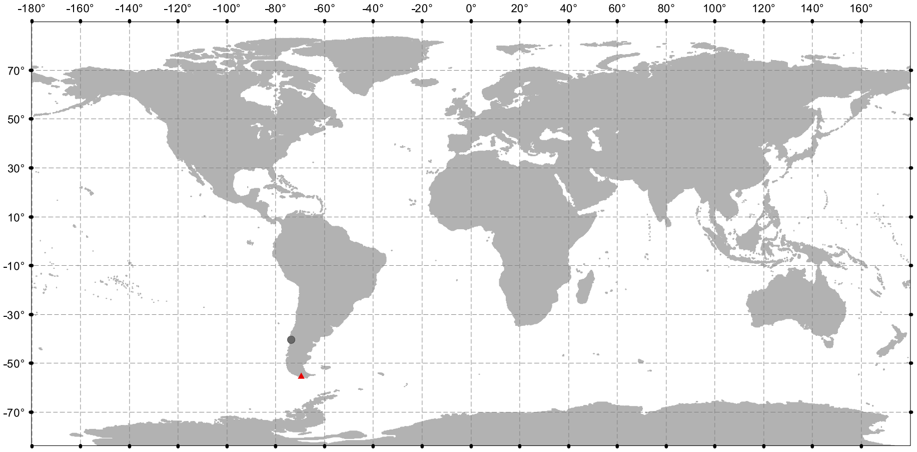


FIG. 172 – Distribution of *Ulota streptodon* worldwide. The red triangle indicates the type locality.

Among the *Ulota* species with multicellular spores, *U. streptodon* resembles the local species *U. billbuckii*, however, the latter has well-developed endostome segments and capsules never puckered at the mouth. All species with multicellular spores have been discussed above in this work (see Notes in *U. gigantospora*), as well as in previous studies (Garilleti *et al.*, 2012). Moreover, *Ulota streptodon* also apparently looks like *U. drummondii*, common in the Northern Hemisphere. Both have erect to flexuose leaves, absent endostome segments, puckered capsule mouth, and densely hairy calyptra. *Ulota drummondii*, however, differs in the more rows (4–6) of hyaline cells with only thickened transverse walls at basal leaf margins, rounded leaf bases, long-cylindrical capsules (2.1–2.5 mm), stomata located on the transition zone between urn and neck and unicellular spores (24–27 μm).

There are only two specimens of *Ulota streptodon* available for us during this work, and thus no noteworthy variation was seen.

Key to *Ulota streptodon* and its closely related species.

1. Spores unicellular, 24–27 μm; leaf cells at basal margins differentiated in more rows (4–6); capsules long-cylindrical, 2.1–2.5 mm; stomata located on the transition zone between urn and neck..*U. drummondii*
1. Spores multicellular, 85–126 μm; leaf cells at basal margins differentiated no more than three rows; capsules cylindrical, 1.3–1.4 mm; stomata located on the urn..2
2. Endostome segments well-developed, 16, broad; capsules never puckered at mouth when dry..*U. billbuckii*
2. Endostome segments absent, sometimes rudimentary; capsules often somewhat puckered at mouth when dry...*U. streptodon*

Additional Specimens Examined: **Chile**. Los Ríos: Cordillera Pelada, Dec. 1932, *A. Hollermager s.n.* (S), 14 Dec. 1932, *A. Hollermager 1668* (PC).

48. **Ulota viridis** Venturi, Öfvers. Finska Vetensk.-Soc. Förh. 35: 43. 1893. Type: Australia. Tasmania: Mt. Wellington, near the springs, on wood, 15 Oct. 1890, *W. A. Weymouth 901* (holotype, TR; isotypes, H4336010! HO!).

Ulota anceps Venturi, Öfvers. Finska Vetensk.-Soc. Förh. 35: 42. 1893. Type: Australia. Tasmania: Mt. Wellington, Springs to Ferntree, 7 Mar. 1891, *W. A. Weymouth 900* (holotype, H; isotype, HO).

Ulota dixonii Malta, Acta Horti Bot. Univ. Latv. 7: 19. 1933. Type: Australia. Tasmania, South part of the Island, Hartz Mountains, on track to Lake Perry, on limbs of tree, alt. 3000 ft, 7 Jan. 1908, *W. A. Weymouth 2299* (holotype, H4336006! isotypes, BM000982389! HO!).

Ulota membranacea D.H. Ashton & R.F. McCrea, Victorian Naturalist 87: 254. 1970. *invalid, no description.*

Ulota novae-seelandiae Sainsbury, Bull. Roy. Soc. New Zealand 5: 223. 1955. Type: New Zealand. North Island, Taranaki, Mt. Egmont, Fantham's Peak Track, on bark of subalpine scrub, at ca. 4000 ft, 16 Jan. 1945, *G. O. K. Sainsbury 10443* (holotype, WELT-M005757!).

Ulota viridis var. *adpressa* Mitt. ex Malta, Acta Horti Bot. Univ. Latv. 7: 22. 1933. ≡ *Ulota appressa* Mitt., Proc. Linn. Soc. New South Wales 30 (Suppl.): 96. 1906. *invalid, cited as synonym.* Type: New Zealand. Otago, Mt Bonpland, on stems of Beech, Jan. 1890, *W. Bell* (lectotype, H, designated by Fife, 2017; isolectotype, CHR).

Plants 0.5–2 cm tall, somewhat slender, yellow to green above, brown to black below. Stems are usually creeping, with erect branches. Leaves erect, flexuose when dry, patent when moist, (1–) 1.2–1.7 (–2.1) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, oblong, (5–) 8–11 (–16) × (3–) 5–8 (–10) μm, thick-walled, with low papillose or smooth; basal inner cells linear, rectangular to vermicular, (15–) 25–34 (–46) × (1–) 2–3 (–4) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in (1–) 3–5 (–8) rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves somewhat longer, (1.7–) 2–2.2 (–2.3) mm. Vaginula sparsely hairy, uniseriate, smooth, hyaline. Seta (2.5–) 3.2–5.2 (–6.5) mm long, often twisted anticlockwise when dry. Capsule long exserted, (1.1–) 1.5–2 mm long. Urn cylindrical, slightly to strongly constricted below the mouth when dry and empty, with eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly or gradually narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the base of the urn or the junction between the urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, often lying on the exothecium, lanceolate, densely papillose outside, finely papillose throughout or striate below, and papillose above inside. Endostome segments 8, linear to narrow-lanceolate, as tall as teeth, uniseriate, 1/2–1/4 width of teeth, hyaline, smooth outside, slightly scabrous or finely papillose inside. Opercula with a short beak. Calyptra mitrate, densely, rarely sparsely hairy. Spores spherical, finely papillose, (19–) 25–33 (–40) μm in diameter.

Illustration: Malta (1933) and Ramsay (2006); figures 173 and 174.

Habitat: It grows on trunks or branches of trees, such as *Acacia*, beech, *Nothofagus*, *Richea*, and *Tasmannia*. There are many records of altitude:

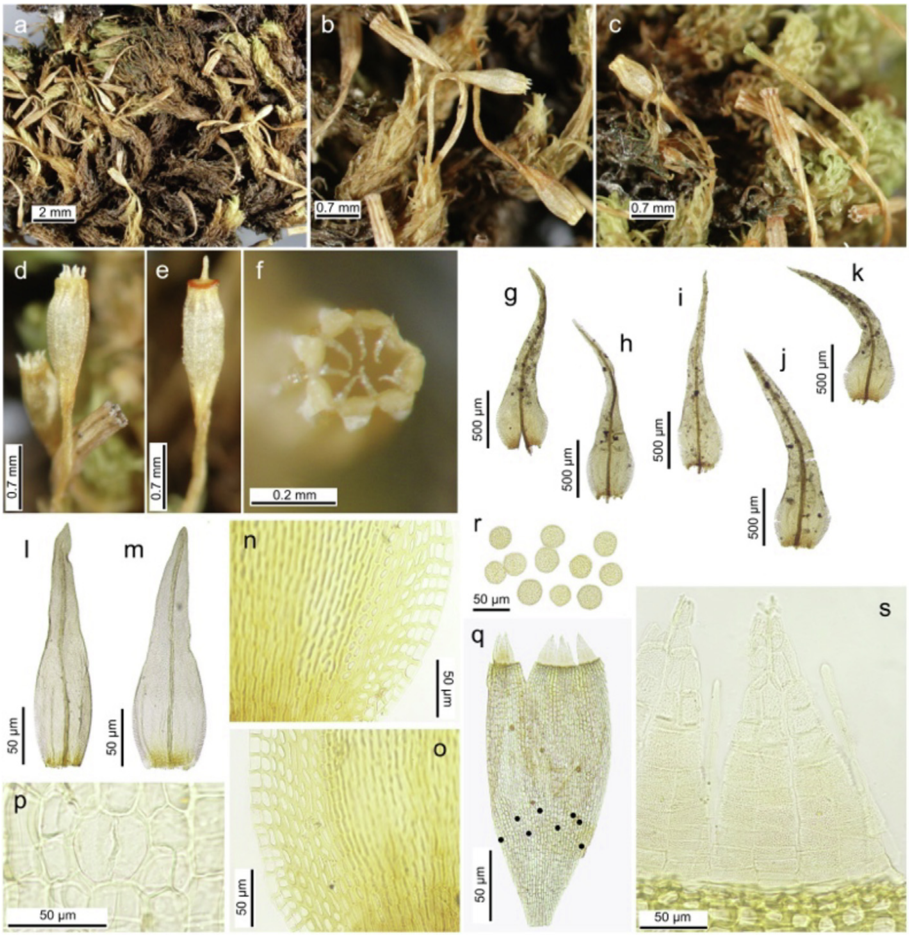


FIG. 173 – *Ulota viridis* Venturi. a–c. Habit. d–e. Capsules in dry. f. Capsule mouth viewed from above. g–k. Leaves. l–m. Perichaetial leaves. n–o. Marginal cells at leaf base. p. Stoma. q. Exothecial wall, with dots indicating stoma position. r. Spores. s. Peristome. (a–f from *D. H. Vitt 10483* [non-type, S], others from *G. O. K. Sainsbury* [non-type, S]).

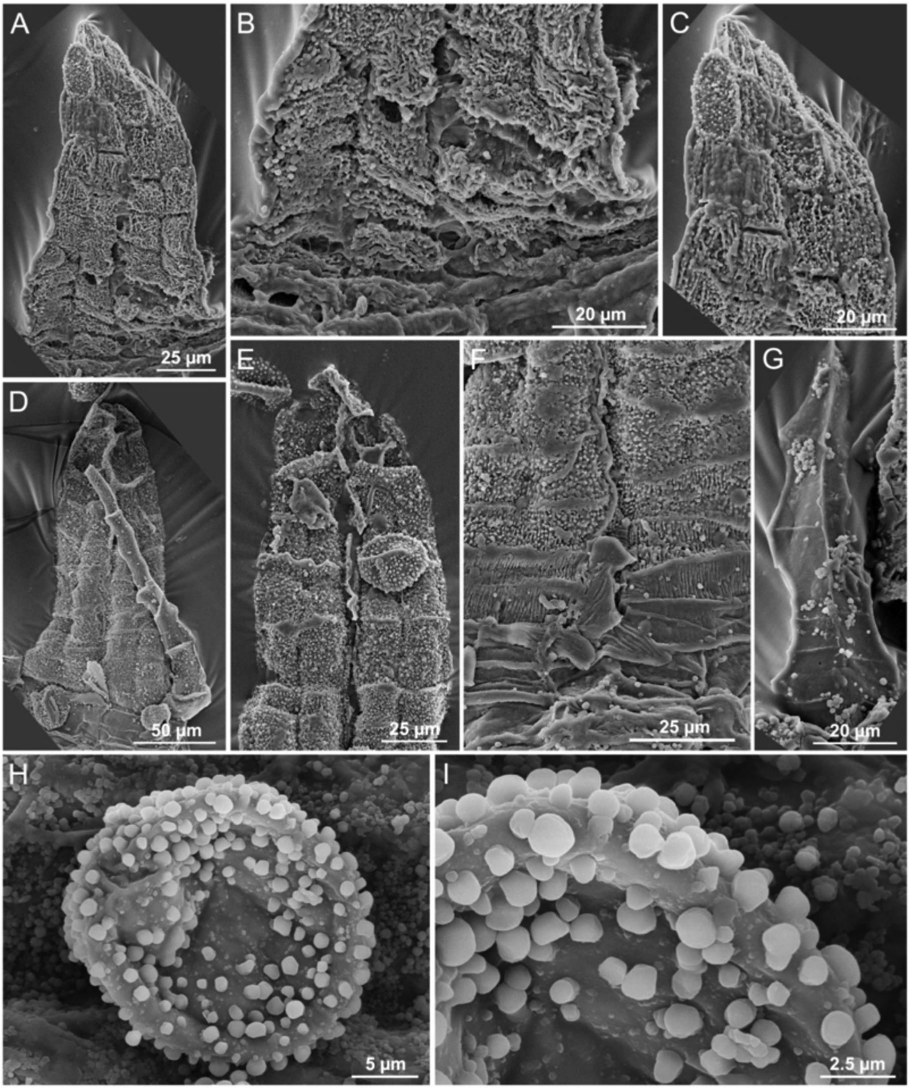


FIG. 174 – *Ulota viridis* Venturi. A, outer view of exostome; B, outer surface of basal exostome; C, outer surface of upper exostome; D, inner view of peristome; E, inner surface of upper exostome; F, inner surface of basal exostome; G, outer surface of endostome; H, a spore; I, surface ornamentation of a spore. (All from the isotype in H).

(152–) 600–1137 (–1500) m. It's occasionally mixed with *Ulota crispa* and *Orthotrichum tasmanicum*.

Distribution: It is restricted to Southeast Australia and New Zealand. Figure 175.

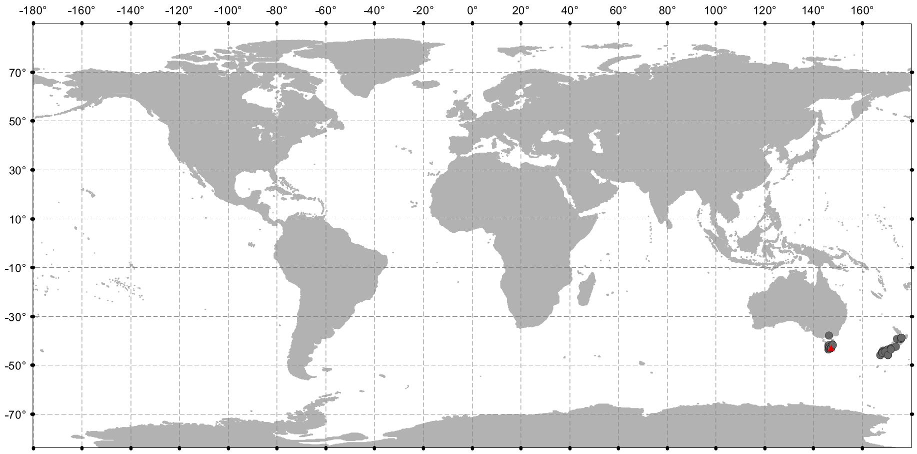


FIG. 175 – Distribution of *Ulota viridis* worldwide. The red triangle indicates the type locality.

Notes: *Ulota dixonii* was treated as a variety of *U. viridis* by Ramsay (2006). She (2006) mentioned that the variety differs from var. *viridis* in the larger and more robust plants, larger lanceolate stem leaves, only 1–3 rows of hyaline cells at basal leaf margins, and spores distinctly verrucose. However, through our observation, these characters are either irregular or minor, which cannot distinguish them clearly, we, therefore, regard *Ulota dixonii* as a synonym of *U. viridis* here, and this is consistent with Fife's recent treatment (2017).

In fact, all sporophytic characters in *Ulota viridis* are not very distinct, such as cylindrical capsules, eight narrow endostome segments, and hairy calyptra, while its gametophytic characters are somewhat special, such as slender plants, creeping stems, and non-crisped leaves. But these "special" gametophytic characters and "common" sporophytic characters provide a unique combination to recognize *Ulota viridis*.

According to the creeping stems, small leaves, small capsules, and yellow rim of opercula in *Ulota viridis*, Malta (1933) considered that it is close to *U. rehmannii* in Euroasia, *U. megalospora* in North America, *U. magellanica* and *U. ventricosa* in South America and *U. reptans* in Asia. All types of specimens of these species have been examined by us except *Ulota ventricosa*. We found that these species indeed mostly share the same characteristics as *Ulota viridis* as mentioned by Malta (1933). However, the differences among them are also distinct; for example, *Ulota rehmannii* differs in the strongly striate exostome teeth and naked or sparsely hairy calyptra, *U. megalospora* in hardly differentiated cells at basal leaf margins and large spores (41–51 μm), *U. magellanica* in hardly differentiated cells at basal leaf margins, 16 wide endostome segments, large spores (36–44 μm) and nearly naked calyptra and *U. reptans* in weakly differentiated cells at basal leaf margins and sparsely hairy calyptra.

The capsule contraction varies greatly, and most materials with strongly constricted capsules are from New Zealand. Few specimens have more than three rows of hyaline cells at leaf basal margins, which is a character used to identify *Ulota dixonii* by Ramsay (2006), but no other regular characters were found by us to distinguish it.

Key to *Ulota viridis* and its closely related species.

1. Endostome segments 16, lanceolate..*U. magellanica*
1. Endostome segments 8, linear to narrow-lanceolate...2
2. Leaf cells at basal margins hardly differentiated, no more than three rows; capsules short, 1–1.4 mm; spores relatively large, 30–51 μm............................3
2. Leaf cells at basal margins often differentiated in 3–6 rows; capsules relatively long, 1–2 mm; spores small, 25–33 μm..4
3. Seta longer, 3–4.5 mm; spores large, 41–51 μm; capsules with long neck...*U. megalospora*
3. Seta relatively short, 2.5–3.2 mm; spores small, 30–38 μm; capsules with short neck...*U. reptans*
4. Exostome teeth prominently variably striate outside; calyptra naked or sparsely hairy; seta relatively short, 2–3.3 mm..*U. rehmannii*
4. Exostome teeth densely papillose outside; calyptra densely hairy; seta longer, 3.2–5.2 mm..*U. viridis*

Additional Specimens Examined: **Australia**. TASMANIA: Mt. Field National Park, 146°35′ E, 42°39′ S, 25 Nov. 1978, *A. V. Ratkowsky* H506 (HO); Mt. Lord, 30 Jan. 1993, *J. Jarman s.n.* (HO); Mt. Wellington, 9 Dec. 1890, *W. A. Weymouth 537* (H), 7 Mar. 1891, *900* (H), 12 Jan. 1890, *s.n.* (S); south of Narcissus Hut, 14 Jan. 2004, *K. Felton s.n.* (HO); the lagoon of New Falls Creek, 11 Dec. 2000, *K. Felton s.n.* (HO). VICTORIA: Mt. Müller, 1895, *C. Treuih & Turtnal Alpŏ s.n.* (H).

New Zealand. AUCKLAND: Pine Hill, Nov. 1889, *W. Bell 9b* (H), Dec. 1890, *16* (H). CANTERBURY: Mt. Cook National Park, 13 Mar. 1980, *J. Lewinsky 2299* (MICH); Mt. Cheeseman, 25 Sep. 1960, *K. W. Allison* 6836 (H, MICH). MANAWATU-WANGANUI: Mt. Ruapehu, Aug. 1934, *L. B. Moore s.n.* (S). NELSON: Saint Arnaud, 14 Nov. 1987, *H. P. Ramsay 32/87* (NSW). SOUTHLAND: Darran Mountains, Gertrude Valley, 168°0′ E, 44°46′ S, *Macmillan BH 90/231* (CHR); Fiordland National Park, 167°23′ E, 45°45′ S, 17 Nov. 1990, *A. J. Fife 9587-1* (CHR). TARANAKI: Egmont National Park, Mt. Egmont, 174°05′ E, 39°18′ S, Dec. 1978, *J. K. Bartlett s.n.* (AK).

49. **ULOTA YAKUSHIMENSIS** Z. Iwats., J. Hattori Bot. Lab. 21: 153. 1959. TYPE: JAPAN. Kagoshima Prefecture, Island Yakushima, between Kosugidani and Hananoego, 10 Apr. 1950, *H. Hasegawa, M. Fukuhara and Fukui 8343*, (holotype, NICH! isotype, NUM!).

Plants ca. 1.3 cm tall, yellow to green on the top, brown to black below. Stems usually branched. Leaves flexuose, rarely crisped when dry, wide-spreading when moist, (1–) 1.4–1.9 (–2.2) mm long; leaf lamina lanceolate, unistratose; leaf base wide, rounded; apex long acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, oblong, (6–) 8–10 (–12) × (5–) 7–9 (–11) μm, thick-walled, with low papillose; basal inner cells rhombic, rectangular and vermiculate, (14–) 18–22 (–27) × (3–) 4–6 (–9) μm, with strongly thickened wall, smooth; basal marginal cells often differentiated in 3–6 rows, hyaline, quadrate to rectangular, with only thickened transverse walls.

Autoicous. Perichaetial leaves somewhat longer, (1.7–) 2.1–2.4 (–2.6) mm. Vaginula not seen. Seta 0.7–1.3 mm long, often twisted anticlockwise when dry. Capsule long exserted, 1.1–1.5 (–1.6) mm long. Urn subglobse, hardly constricted below the mouth when dry and empty, with eight furrows along the entire length. Neck short, abruptly narrowed to the seta. Exothecial cells distinctly differentiated into eight bands, almost as long as an urn, three to four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between urn and neck. Preperistome not seen. Peristome single. Exostome teeth 16, often united into 8 pairs, lanceolate, irregularly erect or spreading to incurved when dry, densely papillose below and striate above on the outside, finely papillose throughout on the inside. Endostome segments are absent. Opercula not seen. Calyptra mitrate, densely to moderately hairy. Spores spherical, very large, multicellular, (60–) 79–91 (–105) μm in diameter.

Illustration: Iwatsuki (1959), Noguchi and Iwatsuki (1989) and Wang and Jia (2012a); figures 176–178.

Habitat: It grows on branches of trees, but no phorophyte was recorded. Three is only one altitudinal record, from 1400 m to 1700 m. No mixed growth has been found in this study.

Distribution: It occurs in Japan; for the previous record from China, see comments below. Figure 179.

Notes: *Ulota yakushimensis* is a very distinct species. It differs from its congeners by a number of characteristics, including flexuose leaves, subglobse capsules, single peristome, and multicellular spores.

Locally, *Ulota yakushimensis* is similar to *U. eurystoma* in leaves with a rounded base and acuminate apex, distinctly differentiated cells at basal leaf margins, capsules not or hardly constricted when dry and not cylindrical in shape, and seta usually becoming hollow and thicker in the upper part. But *Ulota eurystoma* is distinguished by strongly crisped leaves, weakly ornamentated exostome teeth, well-developed endostome segments, and unicellular spores (24–27 μm).

As mentioned above, there are seven recognized species in *Ulota* that have multicellular spores in the world, including *U. novo-guinensis*, *U. membranata*, *U. yunnanensis*, *U. gigantospora*, *U. yakushimensis*, *U. billbuckii*, and *U. streptodon*. Their morphology has been compared detailedly in a previous study (Garilleti *et al.*, 2012) and this work (see Notes of *Ulota gigantospora*). Among them, *Ulota yakushimensis* is the only species with subglobose capsules

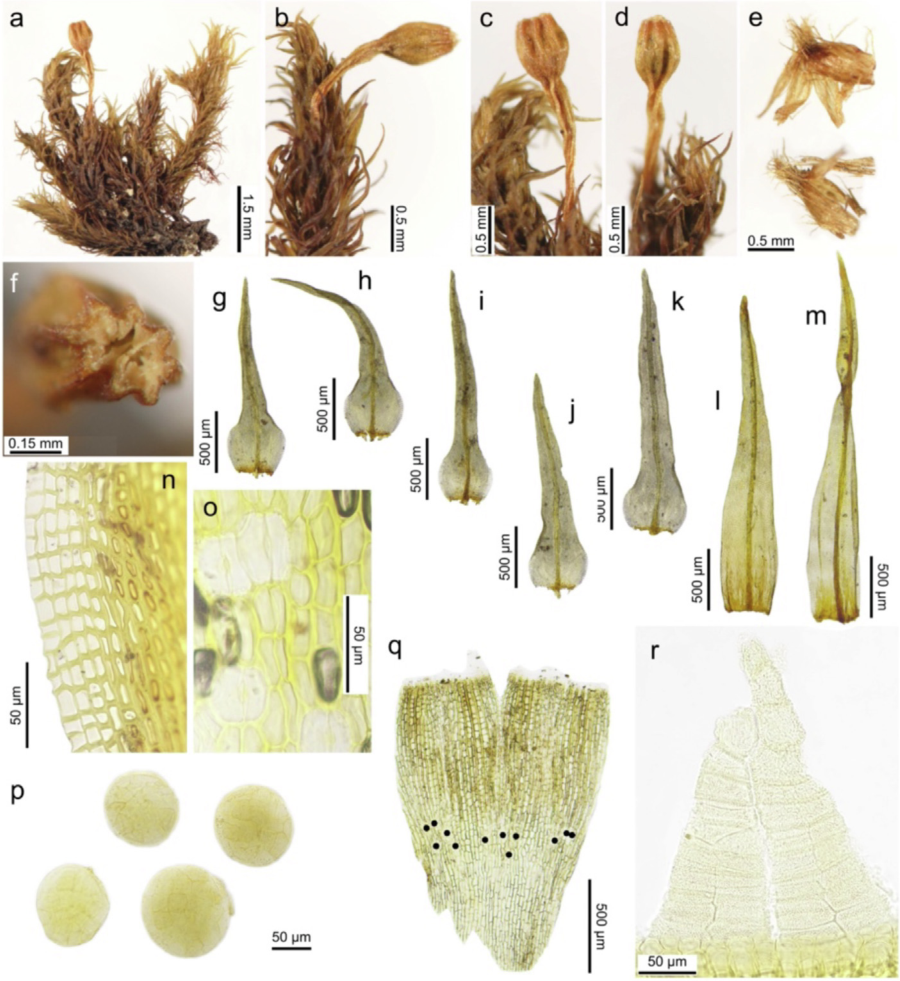


FIG. 176 – *Ulota yakushimensis* Z. Iwats. a–b. Habit. c–d. Capsules in dry. e. Calyptra. f. Capsule mouth viewed from above. g–k. Leaves. l–m. Perichaetial leaves. n. Marginal cells at leaf base. o. Stomata. p. Spores. q. Exothecial wall, with dots indicating stoma position. r. Peristome. (a–f and m–p from holotype in NICH, g–k and q from *Z. Iwatsuki* [non-type, S], l and r from isotype in NUM).

and absent endostome segments. Furthermore, only four species of *Ulota* hitherto have single peristome, including *U. drummondii*, *U. coarctata*, *U. yakushimensis*, and *U. perichaetialis*. The first three species occur in the Northern Hemisphere, and they are more similar in morphology compared with *Ulota perichaetialis* from the Southern Hemisphere. Nevertheless, *Ulota drummondii* differs from *U. yakushimensis* in the long-cylindrical capsules are strongly constricted and

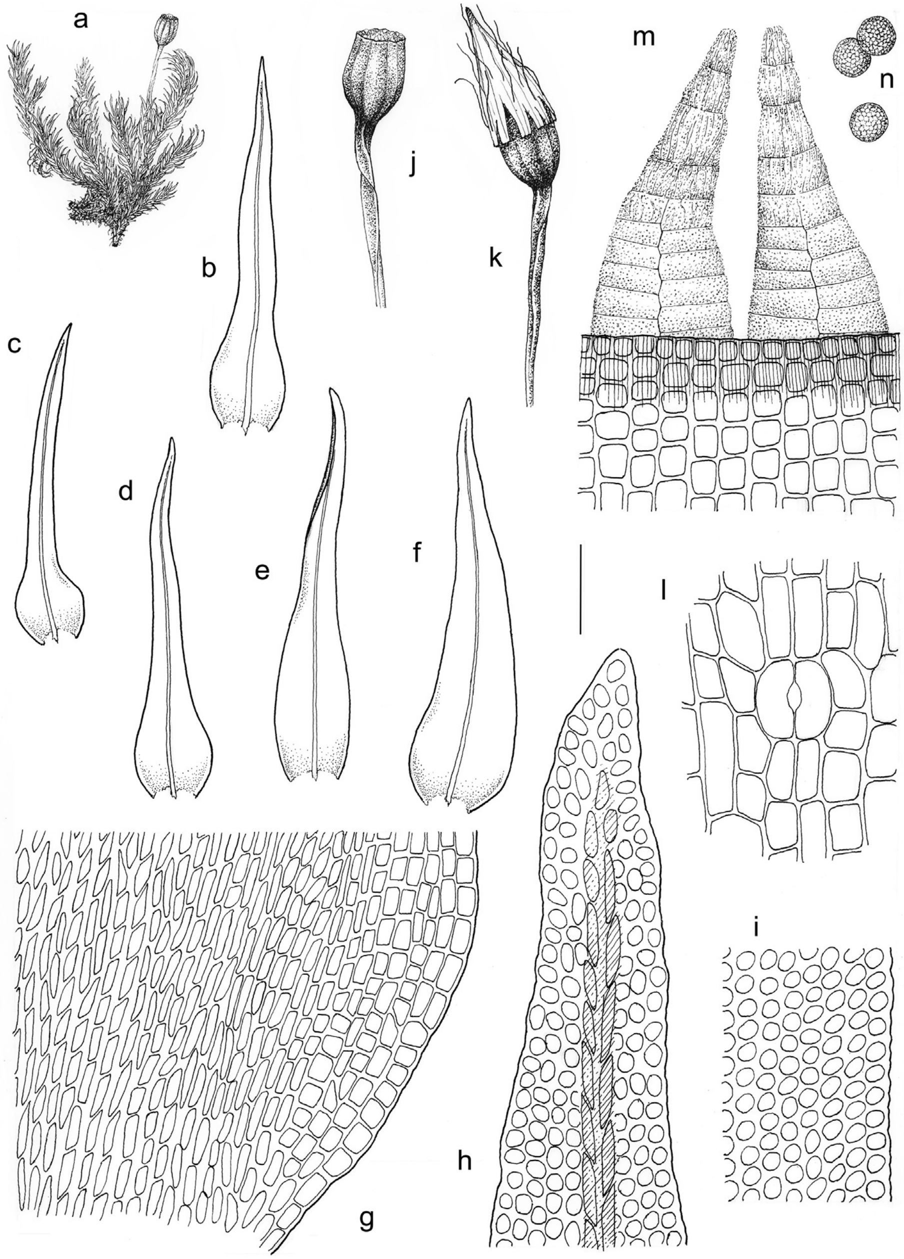


FIG. 177 – *Ulota yakushimensis* Z. Iwats. a. plant; b–d. leaves; e–f. perichaetial leaves; g. basal marginal cells; h. top laminal cells; i. marginal laminal cells; j. an empty capsule in dry; k. a capsule with calyptra; l. stoma; m. a portion of peristome; n. spores. (Scale bar: a, 3.3 mm; b–f, 0.48 mm; g–i and l, 0.04 mm; j–k, 0.95 mm; m, 0.05 mm; n, 0.22 mm. All drawn from holotype in NICH).

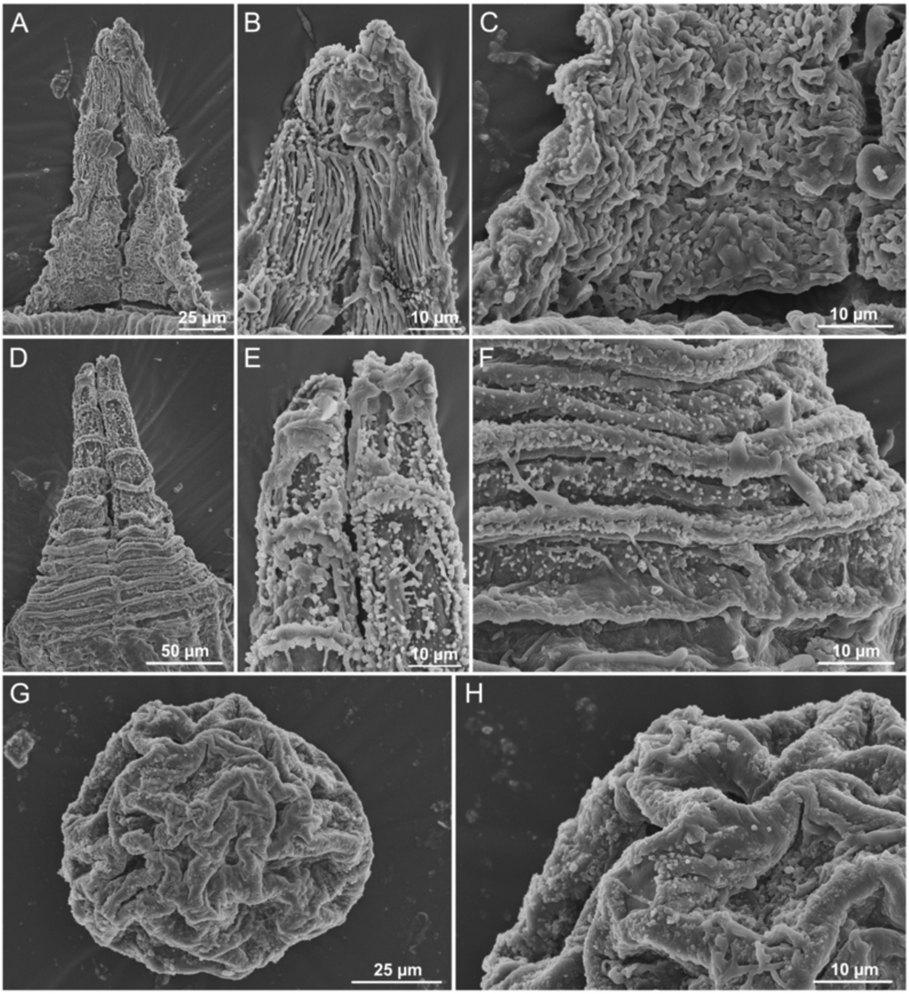


FIG. 178 – *Ulota yakushimensis* Z. Iwats. A, outer view of exostome; B, outer surface of upper exostome; C, outer surface of basal exostome; D, inner view of exostome; E, inner surface of upper exostome; F, inner surface of basal exostome; G, a spore; H, surface ornamentation of a spore. (All from the isotype in NUM).

often with a somewhat puckered mouth when dry, while *U. coarctata* differs in the pyriform capsules strongly constricted only at the mouth, and the less rows (2–4) of hyaline cells at basal leaf margins.

The previous report of *Ulota yakushimensis* from China (Wang and Jia, 2012a) is not confirmed after re-examination during this study, but this still needs further study based on more materials.

No noteworthy variation within *Ulota yakushimensis* was seen.

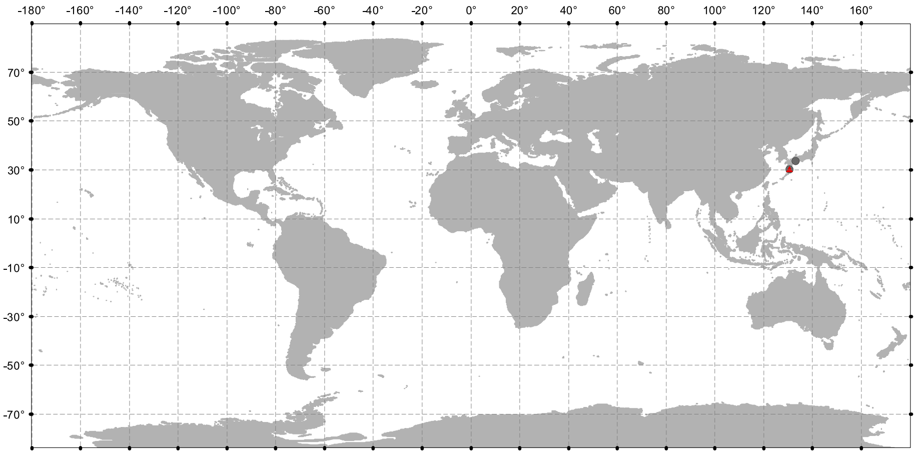


Fig. 179 – Distribution of *Ulota yakushimensis* worldwide. The red triangle indicates the type locality.

Key to *Ulota yakushimensis* and its closely related species.

1. Capsules pyriform, with strongly puckered mouth; leaf hyaline cells at basal margins differentiated in less rows, 2–4 rows.................................*U. coarctata*
1. Capsules long-cylindrical, subglobose or obovoid, sometimes, with slightly to moderately puckered mouth; leaf hyaline cells at basal margins differentiated in more rows, 3–12 rows..2
2. Capsules long-cylindrical, strongly constricted when dry, often with somewhat puckered mouth...*U. drummondii*
2. Capsules subglobose to obovoid, not or hardly constricted when dry, with no or slightly puckered mouth..3
3. Leaves strongly crisped when dry; exostome teeth weakly ornamentated with wrinkle to striolate; endostome segments well-developed and smooth; spores unicellular; capsule mouth not constricted and are the widest part when dry...*U. eurystoma*
3. Leaves often flexuose when dry; exostome teeth strongly ornamentated with densely papillose to papillose-striate; endostome segments absent; spores multicellular; capsule mouth slightly constricted and not the widest part when dry...*U. yakushimensis*

Additional Specimens Examined: **Japan**. Ehime: Mt. Ishizuchi, s. date, *Z. Iwatsuki 44816* (S). Kagoshima: Isl. Yakushima, 5 Dec. 1964, *Z. Iwatsuki, A.J. & Evelyn Sharp 1049* (HYO).

50. **Ulota yunnanensis** F. Lara, Caparrós & Garilleti, J. Bryology 33: 211. 2011. Type: China. Yunnan: Zhongdian (Shangrila) County, N slope of Xiao

Xue Shan (Little Snow Mountain), N of Geza, 28°19′38″ N, 99°45′39″ E, alt. 3845 m. *Abies-Rhododendron* forest; on *Quercus*, 28 May 1993, *D. G. Long 23775*, (holotype, E00266284! isotypes, PE, MO and Herbarium at Universidad Autónoma de Madrid).

Plants 1–2.5 cm tall, yellow to green above, brown below. Stems usually branched. Leaves strongly crisped when dry, erect-patent to patent when moist, (1.3–) 1.6–2.2 (–2.5) mm long, leaf lamina lanceolate, unistratose; leaf base wide, rounded, distinctly concave; apex acuminate; leaf margin plane or partially recurved; costa strong, ending shortly below the apex. Upper and middle laminal cells irregularly rounded, rarely oblong, (7–) 9–11 (–13) × (5–) 7–8 (–9) μm, thick-walled, with 1–2 low papillae per cell; basal inner cells linear, rectangular to elongate-rectangular, (16–) 21–27 (–34) × (3–) 5–8 (–11) μm, with strongly thickened wall, smooth; basal marginal cells weakly differentiated, 1–4 rows, hyaline, quadrate to rectangular, with longitudinal and transversal walls slightly, equally thickened.

Autoicous. Perichaetial leaves a little longer, 2.2–2.5 mm. Vaginula is densely hairy. Seta (3–) 4–5 (–5.5) mm long, often twisted anticlockwise when dry. Capsule long exserted, 1–2.1 (–2.2) mm long. Urn short-cylindrical, slightly, sometimes moderately constricted below the mouth when dry and empty, with eight furrows along the entire length, with prominent ribs alternately. Neck short, abruptly narrowed to the seta. Exothecial cells differentiated into eight bands, almost as long as an urn, usually four cells wide, differentiated cells with only extremely thickened longitudinal walls. Stomata superficial, at the junction between urn and neck. Preperistome not seen. Peristome double. Exostome teeth 16, often united into 8 pairs, recurved when dry, often lying on the exothecium, lanceolate, striate above and densely and finely papillose below on both sides. Endostome segments 8, linear to narrow-lanceolate, as tall as teeth, partially biseriate, 1/3–1/4 width of teeth in the middle, hyaline, smooth outside, slightly scabrous or finely papillose inside. Opercula yellowish, with a short to medium long beak. Calyptra mitrate, naked to sparsely hairy. Spores irregularly spherical, finely papillose, often multicellular, (32–) 46–71 (–103) μm in diameter.

Illustration: Caparrós *et al.* (2011); figures 180 and 181.

Habitat: It grows on trunks of trees, such as *Quercus* and spruce. There are some records of altitude: 3275–3850 (–3950) m. No mixed growth has been found in this study.

Distribution: It is **endemic** to Southwest China. Figure 182.

Notes: *Ulota yunnanensis* is characteristic of the prominent striate at the upper part of exostome teeth, as well as weakly differentiated basal marginal leaf cells, densely hairy vaginula, and multicellular spores.

In *Ulota*, species with multicellular spores are rare, and their morphological differences have been discussed in a previous study (Garilleti *et al.*, 2012) and this work (see Notes of *U. gigantospora*). Among them, *Ulota yunnanensis* is the most similar to *U. gigantospora*, but the latter differs in the densely papillose exostome teeth, often with cancellate near the apex, moderately hairy calyptra and relatively large spores (87–105 μm). Additionally, *Ulota yunnanensis* also resembles the local species *U. robusta* in the few rows of hyaline cells at basal leaf margins and short-cylindrical capsules, which hardly constricted when dry. However, *Ulota robusta* is distinguished by the wide endostome segments, unicellular spores (32–37 μm), and naked vaginula.

The spore size in *Ulota yunnanensis* varies greatly. The diameter of multicellular spores is generally at least 60 μm, and the ones less than 50 μm are only found in *Ulota yunnanensis* hitherto. These small spores sometimes seem to be unicellular, but we still need further study to make sure it.

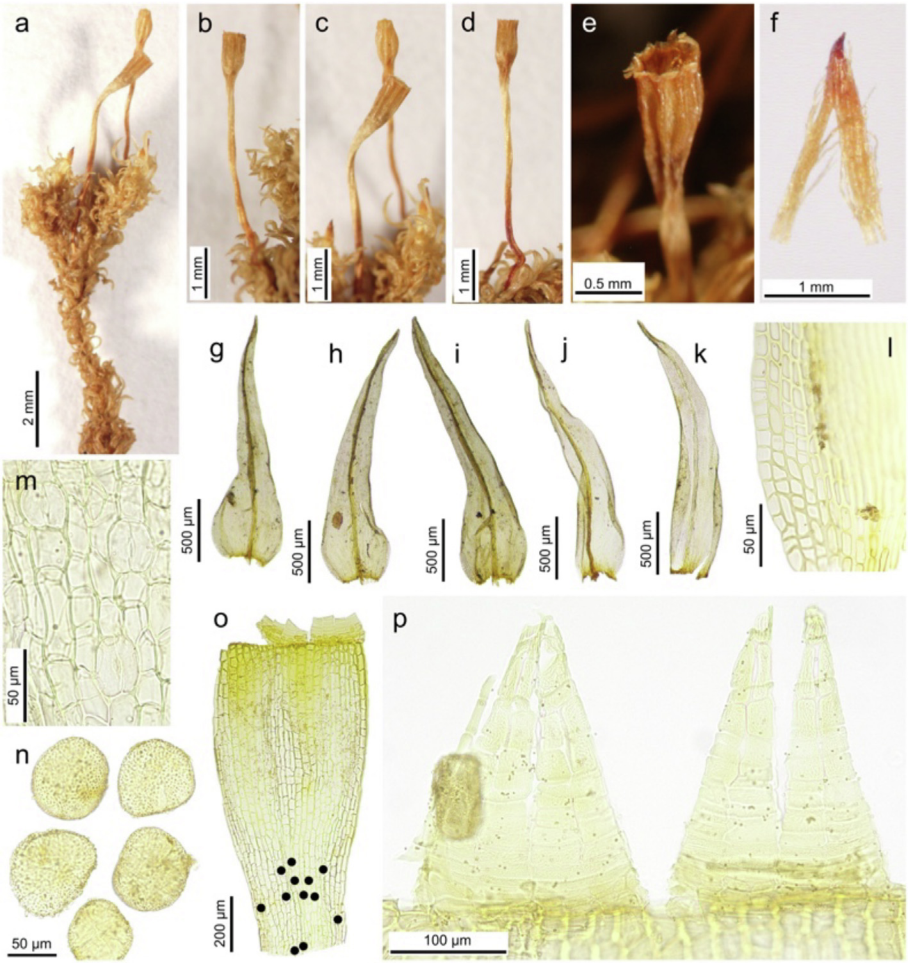


Fig. 180 – *Ulota yunnanensis* F. Lara, Caparrós & Garilleti. a. Habit. b–d. Capsules in dry and empty. e. Capsule mouth. f. Calyptra. g–i. Leaves. j–k. Perichaetial leaves. l. Marginal cells at leaf base. m. Stomata. n. Spores. o. Exothecial wall, with dots indicating stoma position. p. Peristome. (All from the holotype in E except f from *X.-J. Li 81-1366* [non-type, PE]).

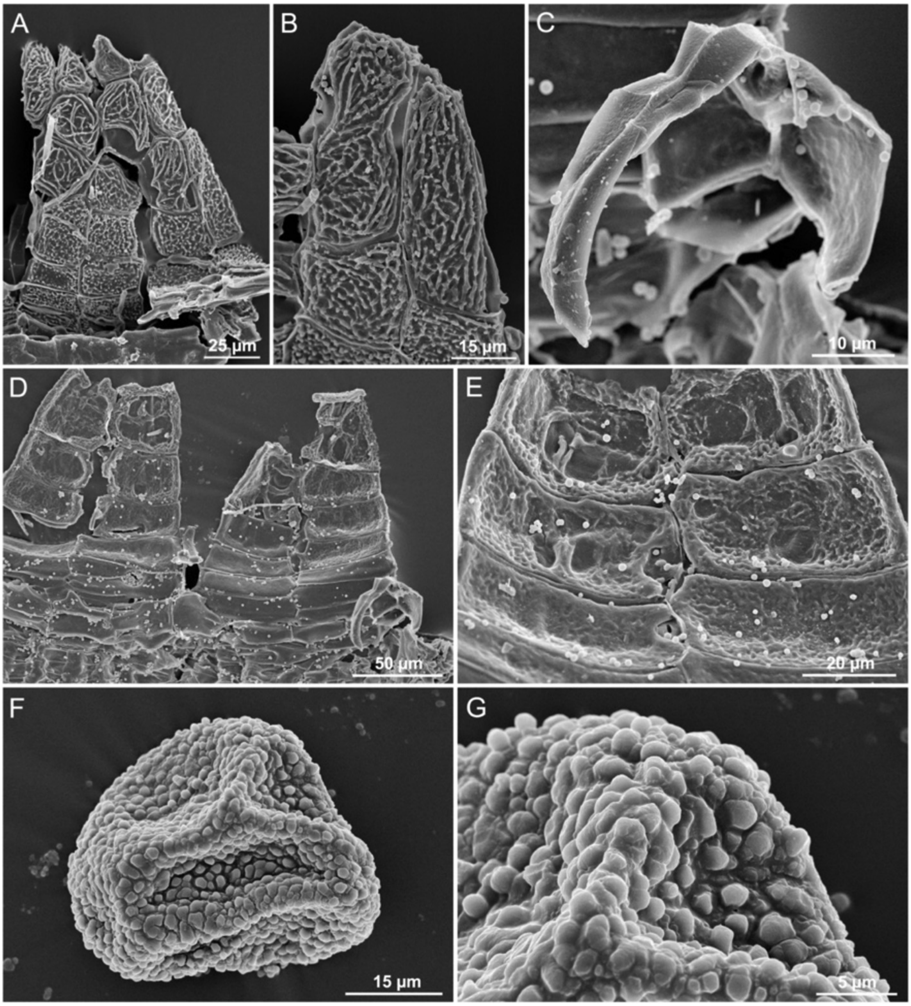


FIG. 181 – *Ulota yunnanensis* F. Lara, Caparrós & Garilleti. A, outer view of exostome; B, outer surface of upper exostome; C, outer surface of endostome; D, inner view of exostome; E, inner surface of upper exostome; F, a spore; G, surface ornamentation of a spore. (All from *L.-S. Wang 83-1173a* [non-type, PE]).

Key to *Ulota yunnanensis* and its closely related species.

1. Spores unicellular, 32–37 μm; endostome segments wide, lanceolate; vaginula naked..*U. robusta*
1. Spores multicellular, 46–105 μm; endostome segments narrow, linear to narrow-lanceolate; vaginula moderately to densely hairy.................................2
2. Exostome teeth with densely papillose and often cancellate at the upper part; calyptra moderately hairy; spores relatively large, 87–105 μm..........................
....*U. gigantospora*

2. Exostome teeth with prominent striate and almost never cancellate at the upper part; calyptra naked to sparsely hairy; spores small, 46–71 μm.. *U. yunnanensis*

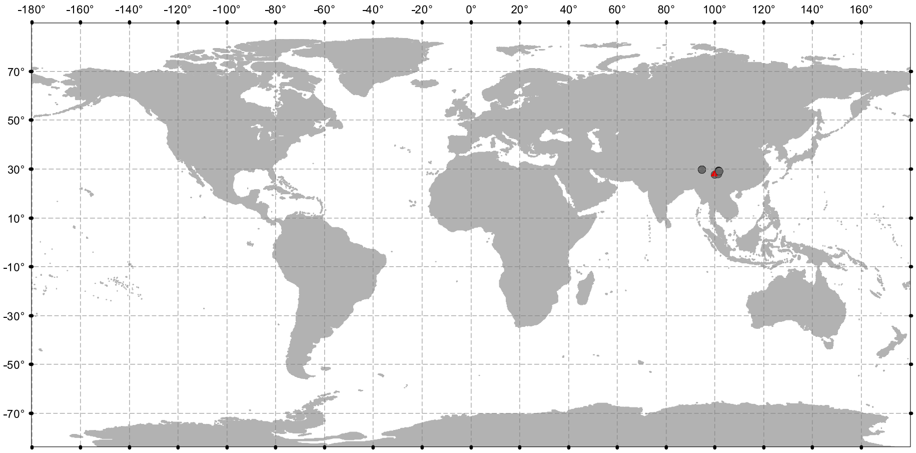


Fig. 182 – Distribution of *Ulota yunnanensis* worldwide. The red triangle indicates the type locality.

Additional Specimens Examined (all in PE): **China**. Sichuan: Jiulong Co., Gonggashan Nature Reserve, 12 Apr. 2021, *Q.-H. Wang 2421*, *2424*, *2391*, *2396*, *2436*, *2438*, 14 Apr. 2021, *2515-2*, Lietahu, 27 Jul. 2021, *Y. Jia & L. Luo 28066-1*, Riluku, 27 Jul. 2021, *Y. Jia & L. Luo 28109*, Wuxuhai, 13 Apr. 2021, *Q.-H. Wang 2478*; Muli Co., Kangwumuchang, 21 Aug. 1983, *M.-Z. Wang 23454*, *23456*, Shangtian, 1983, *M.-Z. Wang 23748-1*, *23754-a*, Xiangyanggou, 23 Aug. 1983, *L.-S. Wang 83-1173-a*. Xizang: Linzhi, Bayi, 7 Aug. 2017, *s. coll.* Yunnan: Zhongdian, Bitahai, 24 Jun. 1981, *X.-J. Li 81-1366.*

4.2.2 Doubtful Species

1. **Ulota orientalis** Fedosov & Ignatova, Novosti Sist. Nizsh. Rast. 52(1): 143, P. I, II, figure 1. 2018. Type: Russia. Khabarovsk Territory, 26 Aug. 2013, *Ignatov & Ignatova 13-1218* (holotype, MHA; isotype, MW).

Description, illustration, habitat, and distribution: see Fedosov and Ignatova (2018).

Notes: *Ulota orientalis*, based on the protologue (Fedosov and Ignatova, 2018), is characteristic by thin-walled rectangular cells at the leaf base, well-differentiated perichaetial leaves, rather small spores, turbinate capsules that are not contracted below the mouth, distinctly striolate exostome teeth, narrow endostome segments, and hairy calyptra. Fedosov and Ignatova (2018) stated that *Ulota orientalis* resembles *U. rehmannii*, but differs in smaller spores (18–22 μm), weakly incrassate basal leaf cells, perichaetial leaves with obtuse to rounded apices and brown capsules. However, we found no significant difference in the thickness of basal leaf cells and capsule color, and furthermore, the distinction in the apices of perichaetial leaves is weak. Therefore, the discrimination between *Ulota orientalis* and *U. rehmannii* is not very clear, especially since they all have funnel-shaped capsules, strongly striolate exostome teeth, non-crisped leaves, conspicuously differentiated cells at basal leaf margins and sparsely hairy calyptra. In addition, the Far East distribution of *Ulota orientalis* falls into the distribution range of *U. rehmannii.* Considering that the original description seems to be based only on the type specimens, the species status of *Ulota orientalis* deserves to be critically re-evaluated. We cannot do anything before the type collection is available.

2. **Ulota pacifica** Fedosov & Ignatova, Novosti Sist. Nizsh. Rast. 52(1): 145, Pl. III, IV, figure 1. 2018. Type: Russia. Sakhalin Region, Iturup Island, 11 Sep. 2015, *Fedosov 15-2-154* (holotype, MW; isotype, MHA).

Description, illustration, habitat, and distribution: see Fedosov and Ignatova (2018).

Notes: According to the protologue (Fedosov and Ignatova, 2018), *Ulota pacifica* is most closely related to *U. japonica.* Both share in thin-walled rectangular cells at the leaf base and small spores. But *Ulota pacifica* is distinguished by short curved seta, capsules that are not constricted below the mouth, and filiform endostome segments. Based on our study, twisted dry seta are very common in the genus *Ulota*, even in *U. japonica.* The endostome segments described by Fedosov and Ignatova (2018) as filiform but are linear for us through their illustration. Besides that, *Ulota pacifica* and *U. japonica* also share in the small plants (0.5–1 cm), non-crisped leaves, many rows of hyaline cells at basal leaf margins, exostome teeth with striate below and papillose above on the inside (see SEM figure in Fedosov and Ignatova, 2018) and somewhat sparsely hairy calyptra. Moreover, *Ulota pacifica* is, in general, geographically consistent with *U. japonica.* In our view, the main differences between them are that in *Ulota pacifica* the capsules are not constricted below mouth when dry (more or less puckered), smooth or scattered papillose leaf lamina, and shorter seta (0.9–1.2 mm). Whether these differences are significant and stable to separate *Ulota pacifica* from other congeners is still uncertain for us due to the lack of specimens, particularly the type materials.

3. **Ulota phyllanthoides** (Müll. Hal.) Kindb., Enum. Bryin. Exot., Suppl. 1 96. 1889. ≡ *Orthotrichum phyllanthoides* Müll. Hal., Bot. Jahrb. Syst. 5: 80. 1883. Type: Kerguelen islands. no other information (not located).

Ulota phyllanthoides has hardly been studied since its original publication. In Müller's protologue (1883), he stated that *Ulota phyllanthoides* is similar to

Orthotrichum jutlandicum Brid. (=*U. phyllantha*), but differs in the relatively longer and wider leaves. However, Malta (1927) considered that *Ulota phyllanthoides* still likely fell into the variation of *U. phyllantha*. During this work, we obtained only three specimens (in PC & L) from Kerguelen islands, but all referred to *Ulota crassifolia* (Hook. f. & Wilson) Hook. f. and should belong to *Orthotrichum* based on our examination. *Ulota phyllanthoides* is very rare not only in specimens but also in other information. Its detailed collection information of type specimens and their locations are still not clear.

4. **Ulota schmidii** (Müll. Hal.) Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 49. 1859. ≡ *Orthotrichum schmidii* Müll. Hal., Bot, Zeit.. Berlin 11: 60. 1853. Type: India. Mt. Nilghiri, *Schmids*, (holotype, H!).

The lectotype consists of only two stem apices (figure 183). Leaves flexuose when dry, lanceolate from a broader base, acuminate; costa strong, percurrent or ending near the apex; upper and middle laminal cells irregularly rounded, thick-walled, with about 1 or 2 short papillae per cell; basal inner cells rhombic, rectangular, smooth, thick-walled; basal marginal cells often differentiated in 7–10 rows hyaline band, quadrate to rectangular, with thickened transverse walls. Sporophytic characters in the protologue are described roughly, including a narrow-pyriform capsule with constricted mouth and 8-ribbed when empty and dry and hairy calyptra. No other specimen and description of this name are available so far. Consequently, *Ulota schmidii* is here regarded as a dubious name.

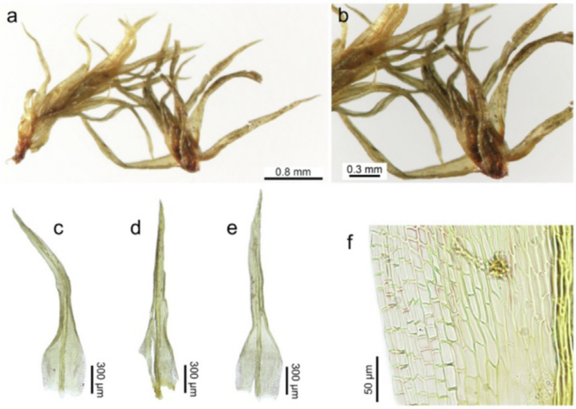


Fig. 183 – *Ulota schmidii* (Müll. Hal.) Mitt. a–b. Habit. c–e. Leaves. f. Marginal cells at leaf base. (All from the lectotype in H).

5. **Ulota ventricosa** (Müll. Hal.) Malta, Acta Horti Bot. Univ. Latv. 2: 180. 1927. ≡ *Zygodon ventricosus* Müll. Hal., Linnaea 18: 668. 1845. Type: “in agro Chilensi, ubi legit Philippi” (not located).

Ulota ventricosa has rarely, if ever, been mentioned in the literature. Malta (1927) cited only two specimens in his protologue (*Philippi s.n.* & *P. Dusén s.n.*), and both were deposited in B herbarium. But we have not obtained any information about them by requesting a loan or searching their herbarium database online, nor in any other herbaria consulted. Only a non-type specimen as *Ulota ventricosa* (Fuegia, Beagle Canal, leg. *M. Gůsinde 357*, Mar. 1922) was found in S (no barcode) so far, but the material is little, consisting of three incomplete branches, and its morphology agrees well with *Orthotrichum bicolor* Thér., rather than *Ulota* species. But this is not the type and thus cannot be used to define *Ulota ventricosa*. In fact, *Ulota ventricosa*, in Malta's protologue (1927), has undifferentiated basal leaf margin, eight pairs of exostome teeth, and sixteen endostome segments. It was considered by Malta (1927) to be related to *Ulota magellanica*, but *U. ventricosa* differs in the wide-spreading leaves and naked calyptra. These distinctions, however, are obviously weak, and thus it is most likely to be a synonym of *Ulota magellanica*. Although Malta (1927) gave a detailed description and illustration of *U. ventricosa*, considering it has not been reported for quite a long time, it is not possible for us to settle the taxonomic position of this taxon only from the protologue.

Chapter 5

Result and Discussion

5.1 Taxonomy

A total of 55 *Ulota* species reported before we prepared this book, of which 50 are recognized here, with two new synonyms and four new type designations. The specimens from Africa, and Central and West Asia are very limited in this study and hence the investigation of these areas is still largely insufficient.

Although the revision of *Ulota* has been completed, there are still some specimens we are unsure which species they belong to. They often have characters between two species and thus are doubted by us to be hybrids. After all, hybridization is likely to be common in *Ulota* due to the frequent occurrence of sexual reproduction and the prevalence of mixed growth. Fedosov and Ignatova, (2018) mentioned similar cases in their study of *Ulota* in Russia.

5.2 Habitats

Based on the climatic zone classification of IPCC (2006), most *Ulota* species occur in the warm or cool temperate moist zones, a few in the tropical wet or moist zones or boreal moist zones. This agrees well with the statement of Vitt *et al.* (1993) that "species of *Ulota* are mostly confined to moist forests".

The altitude of most *Ulota* species is below 2000 m, but a few ones can exceed 3000 m, including *U. gigantospora*, *U. latisegmenta*, *U. morrisonensis* and *U. yunnanensis* from China, *U. robusta* from the Himalayas region, *U. angusti-limbata*, *U. novo-guinensis* and *U. rubella* from Papua New Guinea, and *U. splendida* from Papua New Guinea and Malaysia (figure 185). All these species occur in or near Asia. There are seven *Ulota* species that generally occur at an altitude less than 500 m, including *U. bruchii*, *U. larrainii*, *U. luteola*, *U. maltiana*, *U. obtusiuscula*, *U. phyllantha* and *U. streptodon*. Among them, *U. bruchii.* and *U. obtusiuscula* are from North Hemiphere, *U. larrainii*, *U. luteola*, *U. maltiana,* and *U. streptodon* are from South America, while *U. phyllantha* distributes on both hemispheres.

DOI: 10.1051/978-2-7598-2911-8.c005
© Science Press, EDP Sciences, 2023

Most species of *Ulota* are exclusively epiphytic, and two species are occasionally saxicolous (*U. laticiliata* and *U. cochleata*), one species grows commonly on both trees and rocks (*U. phyllantha*), two species are mainly saxicolous (*U. curvifolia* and *U. hutchinsiae*), and one species is only found on sandstone (*U. ecklonii*). Epiphytic species often grow on the trunk or branches of trees or shrubs (figure 184). There are not many records of their phorophytes, but they still involve more than 60 species, of which the most frequent ones, in turn, are *Nothofagus*, *Alnus*, *Pinus,* and *Salix*. *Nothofagus* is a common phorophyte for *Ulota* species from South Hemisphere, while *Alnus*, *Pinus,* and *Salix* are common phorophytes for these from North Hemisphere. Almost all other species of phorophytes have been recorded no more than three times so far.

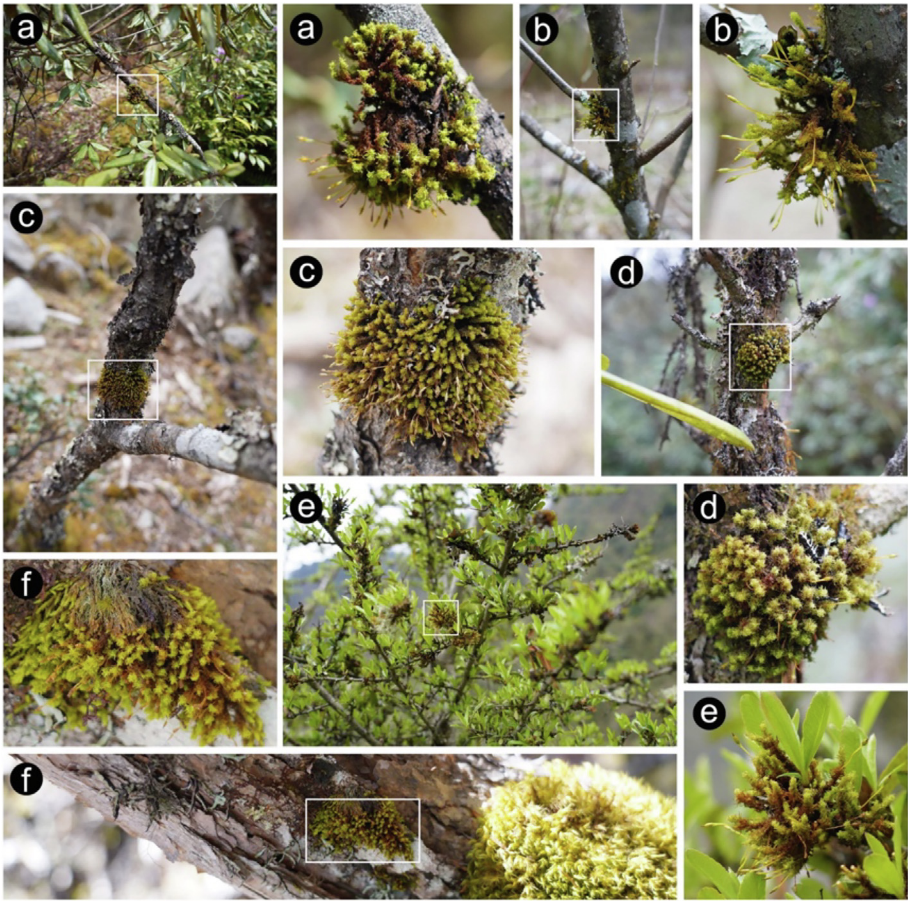


Fig. 184 – Habitats of *Ulota*. In the white boxes are the populations of *Ulota* and their magnifications are next to them with the same letter. a, *U. intermedia* (*Q.-H. Wang 2557*, PE); b, *U. panchengiana* (*Q.-H. Wang 2265*, PE); c, *U. yunnanensis* (*Q.-H. Wang 2424*, PE); d, *U. crispa* (*Q.-H. Wang 2578*, PE); e, *U. panchengiana* (*Q.-H. Wang 2556*, PE); f, *U. yunnanensis* (*Q.-H. Wang 2391*, PE). All photos are taken from China.

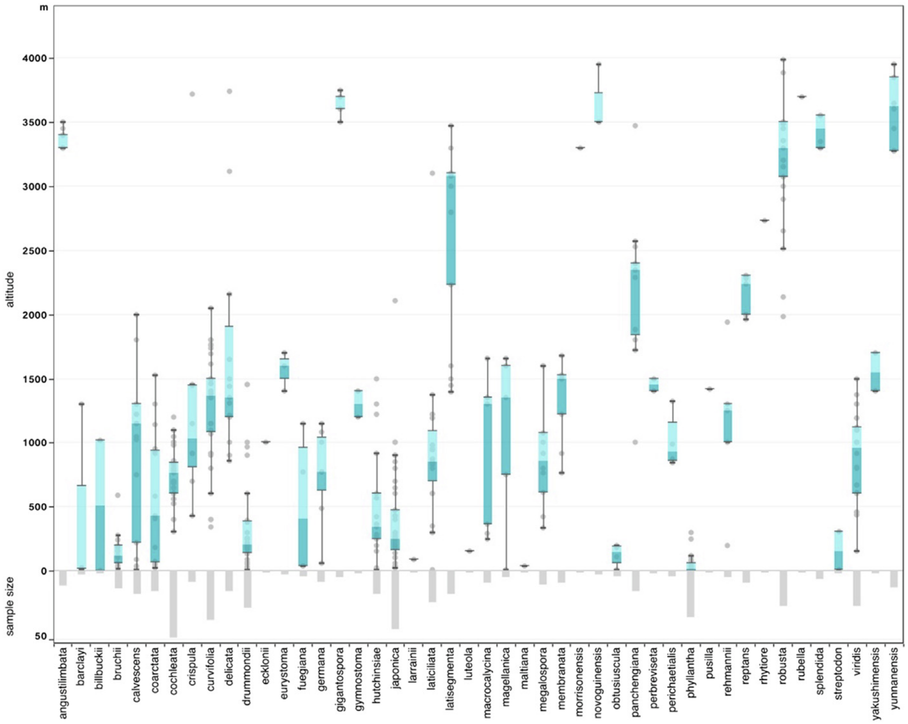


Fig. 185 – Altitudinal range of the genus *Ulota*.

5.3 Geographic Distribution

Generally, the *Ulota* is a cosmopolitan genus, and the species number in North Hemisphere is higher than that in South Hemisphere (31 *vs.* 23). Within *Ulota*, most species occur in different countries on the same continent, some are only restricted to one country, and some can be present across continents in the same hemisphere, only a few can further extend to different hemispheres, including *U. crispa* and *U. phyllantha* (table 2).

Tab. 2 – Worldwide distribution of *Ulota* species. IC = international but same continent, IH = intercontinental but same hemisphere and BI = both hemispheres and intercontinental.

Species	Distribution	Species	Distribution
U. angusti-limbata	endemics-Papua New Guinea	*U. macrocalycina*	IC
U. barclayi	IC	*U. macrodontia*	IC
U. billbuckii	IC	*U. magellanica*	IC
U. bruchii	IC	*U. maltiana*	endemics-Chile
U. calvescens	IC	*U. megalospora*	IC
U. coarctata	IH	*U. membranata*	IC

TAB. 2 – (continued).

Species	Distribution	Species	Distribution
U. cochleata	endemics-Australia	*U. morrisonensis*	endemics-China
U. crispa	BI	*U. novo-guinensis*	endemics-Papua New Guinea
U. crispula	IH	*U. obtusiuscula*	IC
U. curvifolia	IH	*U. panchengiana*	endemics-China
U. delicata	IC	*U. perbreviseta*	IC
U. drummondii	IH	*U. perichaetialis*	endemics-New Zealand
U. ecklonii	IC	*U. phyllantha*	BI
U. eurystoma	endemics-Japan	*U. pusilla*	IC
U. fuegiana	IC	*U. pycnophylla*	IC
U. germana	IH	*U. rehmannii*	IH
U. gigantospora	endemics-China	*U. reptans*	IC
U. gymnostoma	endemics-China	*U. rhytiore*	endemics-El Salvador
U. hutchinsiae	IH	*U. robusta*	IC
U. intermedia	IH	*U. rubella*	endemics-Papua New Guinea
U. japonica	IC	*U. splendida*	IC
U. larrainii	endemics-Chile	*U. streptodon*	endemics-Chile
U. laticiliata	IC	*U. viridis*	IC
U. latisegmenta	endemics-China	*U. yakushimensis*	IC
U. luteola	IC	*U. yunnanensis*	endemics-China

The genus *Ulota* is hitherto reported from all continents except for Antarctica (figure 186). The general distribution pattern in each continent is described as follows. **Asia**: There are two distribution centers in this region; one is the Yangtze River region in China, from the eastern coast to the western high mountains, and the other is Japan and its adjacent northern region. The latitude is between 25° and 45° north. A total of 21 confirmed species occur in this region. **Oceania**: Almost all *Ulota* species in this region are concentrated on Tasmania island in Australia and New Zealand, which are located at 35°–45° south latitude. Eleven species are confirmed by us in this region. **Europe**: *Ulota* species are widespread in this region but few in southern and eastern Europe. A total of 11 confirmed species occur in the range of 45°–70° north latitude. **Africa and surrounding islands**: Only two sites are hitherto reported from the African continent, one in Cape Town, South Africa, and the other in South Sudan. The islands around the continent, including Madagascar, Reunion Island, and Madeira Islands, all have a few records. Only three confirmed species have been reported from this region so far. **North America**: The distribution of *Ulota* in this region is mainly concentrated in the east and west coasts, and the Great Lakes area, at north latitude from 35° to 60°. Eleven confirmed species occur in this region. **South America**: Most species occur in southern South America, from central

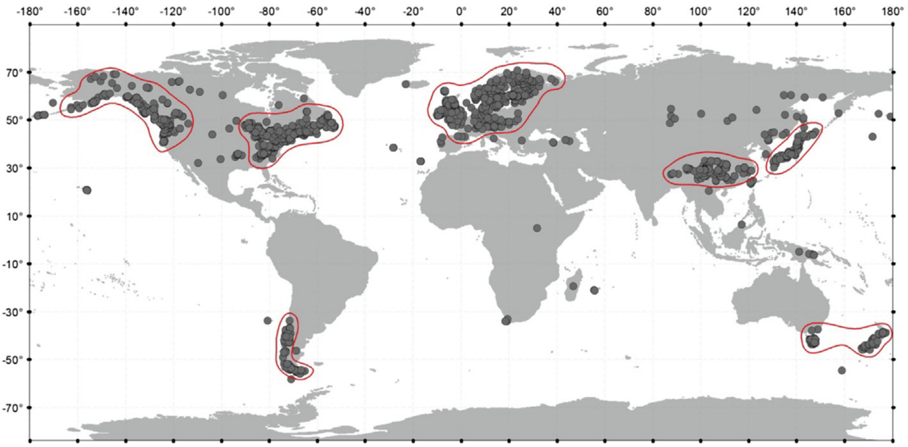


Fig. 186 – Worldwide distribution of *Ulota*, with seven distribution centers indicated here.

Chile to Tierra del Fuego, at south latitudes from 35° to 55°. Fourteen *Ulota* species are confirmed by us in this region. To sum up, there are seven distribution centers of *Ulota* in the world (figure 186), of which southern South America has the highest species diversity (14 sp.) and the highest endemism rate (11 sp.), which is consistent with the statement of Garilleti *et al.* (2015).

5.4 Phylogeny and Evolution

The phylogeny of the genus *Ulota* has not been studied until recently (Garilleti *et al.*, 2021; Wang *et al.*, 2021; Plášek *et al.*, 2015; Goffinet *et al.*, 2004). All molecular evidence so far indicates that *Ulota* is not monophyly, and therefore within it, *U. phyllantha* and *U. calvescens* have been recently segregated as new genera *Plenogemma* Plášek, Sawicki & Ochyra (Plášek *et al.*, 2015) and *Atlantichella* F. Lara, Garilleti & Draper (Draper *et al.*, 2021).

The infrageneric phylogeny of *Ulota* s.tr. has been published most recently (Draper *et al.*, 2021; Wang *et al.*, 2021; figure 187). It contains two clades, one is mainly composed of species from North Hemisphere, and the other is mainly composed of species from South Hemisphere. The interspecific relationship within these two subclades has not been well resolved (figure 187), which maybe because of the insufficient DNA information used in these two studies, and the genome data are expected in the future. Additionally, the species sampling in the current studies is also obviously limited, with about 20 species.

In the family Orthotrichaceae, *Ulota* s.l. is close to *Orthotrichum* s.l. with superficial stomata; the latter has recently been divided into two genera, *i.e. Lewinskya* and *Pulvigera* (Lara *et al.*, 2016; Plášek *et al.*, 2015). Since all species in *Ulota* s.l. have superficial stomata, they and *Lewinskya* and *Pulvigera* form a clade of phaneroporous species with strong support. The internal relationship within this clade has not been well resolved, especially the position of *Plenogemma* and

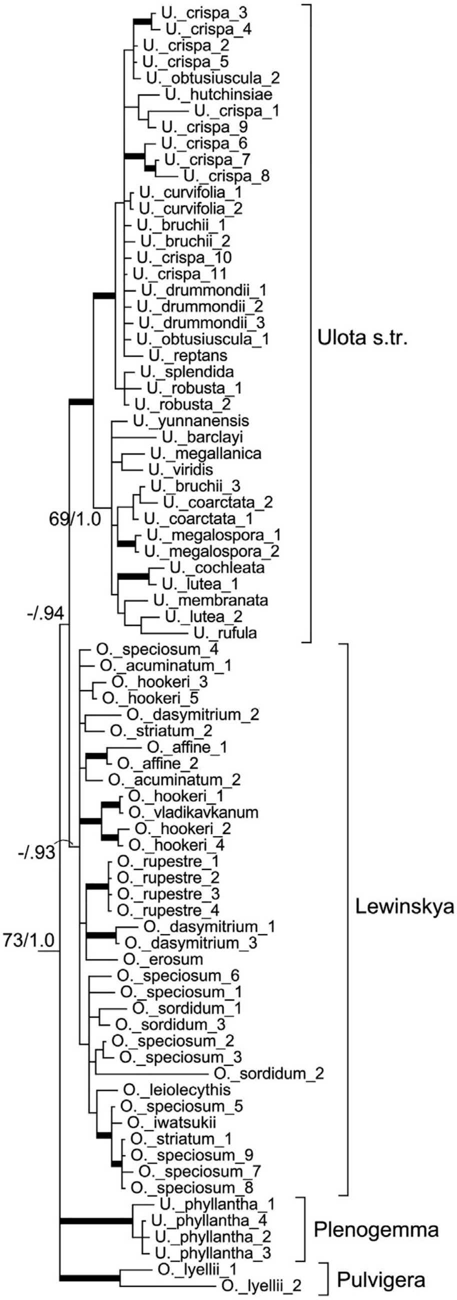


FIG. 187 – Phylogeny of *Ulota* s.l. and phaneroporous species in *Orthotrichum* s.l. based on six DNA regions (nuclear 26S, mitochondrial *nad*5, and plastid *trn*L-F, *psb*A-*trn*H, *atp*B-*rbc*L, and *rps*4) (modified from Wang *et al.*, 2021). Thick branches indicate maximum likelihood (ML) bootstrap support ≥85% and Bayesian inference posterior probability ≥95%. Support values of remaining key branches are shown (ML bootstrap/Bayesian posterior probability). –, branches with <50% support.

Pulvigera (figure 187). Until recently, the results in Draper *et al.* (2021) indicated that *Plenogemma* was sister to *Ulota* s.tr. and *Pulvigera* was the earliest divergence in the whole clade of phaneroporous species.

As mentioned above, the peristome in *Ulota* is very diverse, but the possible evolutionary process between them has not been studied. Contrarily, the other two closely related genera, *i.e.* *Orthotrichum* s.l. (Lewinsky, 1993) and *Zygodon* (Calabrese, 2006), have remarkable reduction tendencies in peristome according to morphological studies. In particular, Lewinsky, (1993) has shown the possible evolutionary pathways in detail and illustrated them. Through many years of taxonomic study, we consider that the peristome in *Ulota* is very similar to that of *Orthotrichum* s.l., with a similar reduction trend. Here, we divide them into six groups:

1. Exostome teeth present, endostome segments 16 and broad (*U. billbuckii*, *U. larrainii*, *U. latisegmenta*, *U. magellanica*, *U. membranata*);
2. Exostome teeth present, endostome segments 16 and narrow (*U. delicata*, *U. maltiana*, *U. morrisonensis*, *U. novo-guinensis*, *U. phyllantha*, *U. pusilla*);
3. Exostome teeth present, endostome segments eight and broad (*U. laticiliata*, *U. robusta*);
4. Exostome teeth present, endostome segments eight and narrow (*U. angusti-limbata*, *U. barclayi*, *U. bruchii*, *U. calvescens*, *U. cochleata*, *U. crispa*, *U. crispula*, *U. curvifolia*, *U. ecklonnii*, *U. eurystoma*, *U. fuegiana*, *U. germana*, *U. gigantospora*, *U. hutchinsiae*, *U. intermedia*, *U. japonica*, *U. luteola*, *U. macrocalycina*, *U. macrodontia*, *U. megalospora*, *U. obtusiuscula*, *U. panchengiana*, *U. perbreviseta*, *U. pycnophylla*, *U. rehmannii*, *U. reptans*, *U. rubella*, *U. splendida*, *U. viridis*, *U. yunnanensis*);
5. Exostome teeth present, endostome segments rudimentary or absent (*U. coarctata*, *U. drummondii*, *U. perichaetialis*, *U. streptodon*, *U. yakushimensis*);
6. Exostome teeth absent, endostome segments rudimentary or absent (*U. gymnostoma*, *U. rhytiore*).

The possible evolutionary pathways of these six groups are shown in figure 188. The current molecular evidence (Draper *et al.*, 2021; Wang *et al.*, 2021; Plášek *et al.*, 2015; Goffinet *et al.*, 2004) is still far from revealing the peristome evolution in *Ulota* due to the limited sampling and the poor resolution of interspecific relationship, and further study is urgently expected.

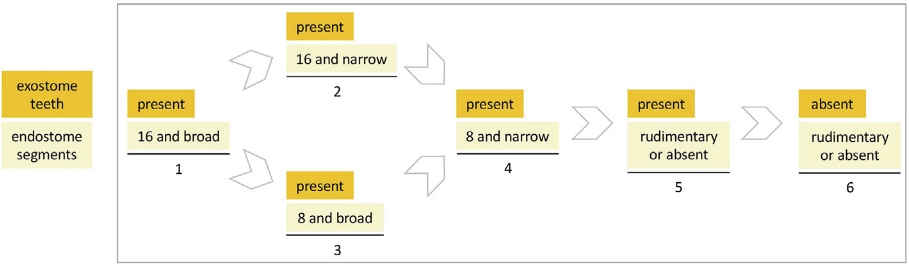


FIG. 188 – Possible evolutionary pathways of peristome in *Ulota*. The number corresponds to the above six groups of peristome.

Acknowledgements

This book is a summary of a study that has lasted for sixteen years since Q.H.W. pursued her PhD supervised by Y.J.. During these years, many people have contributed to this study, and the authors want to thank them all. Some of them deserve special mention. First of all, most specimens used in this study were obtained by loan, and we, therefore, thank all the curators and staff of these herbaria, including AKPM, AM, B, BBSUK, BAU, BISH, BM, BP, C, CANM, CHR, DUKE, E, FH, FI, GACP, GNUB, H, HBG, HIRO, HO, HYO, IBK, IFP, JE, KUN, KYO, L, M, MICH, MO, NICH, NSW, NY, OSA, PC, PE, PRE, RB, S, TNS, UBC, UC, and WELT. We are deeply grateful to the curators and staff of E, HBG, HO, MICH, NSW, S, and UBC for their generously lending of more than one hundred specimens of *Ulota*. During this study, we also received some specimens as a gift from Mamtimin Sulayman at Xinjiang University and warmly addressed our thanks to him here. Many other specimens were studied by Q.H.W. during her one-year visit to the Botanical Museum (H), Finnish Museum of Natural History, with the support of the China Scholarship Council. She is, therefore, very grateful to everyone in the museum for their great help during her stay. In addition, there also include her short-term visits to the S, BM, PC, and FI. Many thanks to the curator and staff of these herbaria for their help during her visit. We also thank Mu-Sen Guo for his beautiful line drawings, Yang Han (Capital Normal University) for his help in measuring a large number of morphological characters, Yang Liu (Shenzhen Fairy Lake Botanical Garden) for helping to find some references, Mei–Zhi Wang for her technical assistance in SEM, Qin Zuo (Shenzhen Fairy Lake Botanical Garden) for the Japanese translation of a reference, Bernard Goffinet and Dale H. Vitt for their valuable suggestions when reviewing the manuscripts related to this study.

Literature Cited

Āboliņa A. (1968) *Mosses of latvian SSR.* Zinātne, Rīga. (in Russian).

Albertos B., Garilleti R., Mazimpaka V. (2008) Reëvaluation of *Orthotrichum rhytiore* (Orthotrichaceae), *Bryologist* **111**, 323.

Albertos B., Lara F., Garilleti R., Mazimpaka V. (2000) Distribution and abundance of corticolous species of the genus *Ulota* (Orthotrichaceae, Musci) in the NW Iberian Peninsula, *Nova Hedwigia* **70**, 461.

Aleffi M., Tacchi R., Cortini-Pedrotti C. (Eds.) (2008) Check-list of the hornworts, liverworts and mosses of Italy, *Bocconea* **22**, 5.

Allen B. H. (2002) Moss flora of Central America, Part 2. Encalyptaceae-Orthotrichaceae, *Monogr. Syst. Bot. Missouri Bot. Gard.* 90.

Allorge P., Persson H. (1938) Mousses nouvelles pour les Açores, *Monde Pl.* **39**, 25.

Anderson L. E., Crum H. A., Buck W. R. (1990) List of the Mosses of North America North of Mexico, *Bryologist* **93**, 448.

Ångström J. (1872) Förteckning och beskrifning öfver mossor, samlade af Professor N. J. Andersson under Fregatten Eugenies verldsomsegling åren 1851–53. I–III, *Öfvers. Kongl. Vetensk.-Akad. Förh.* **29**(4), 3.

Augier J. (1966) *Flore des Bryophytes.* Paul Lechevalier, Paris.

Bardunov L. V. (1974) *Listostebel'nye Mkhi Altaya i Sayan.* Izdatel'stvo Nauka, Novosibirsk.

Bartram E. B. (1942) Third Archbold Expedition mosses from the Snow Mountains, Netherlands New Guinea, *Lloydia* **5**, 245.

Bartram E. B. (1945) Mosses of the Morobe District, northeast New Guinea, *Bryologist* **48**, 110.

Bartram E. B. (1959) Contribution to the mosses of the highlands of eastern New Guinea, *Brittonia* **11**, 86.

Bescherelle É. (1885) Mousses nouvelles de l'Amérique australe, *Bull. Soc. Bot. France* **32**, liv.

Bescherelle É. (1892) Musci Yunnanensis. *Ann. Sci. Nat., Bot.*, sér. 7, **15**, 47.

Bescherelle É. (1893) Nouveaux documents pour la flore bryologique du Japon. *Ann. Sci. Nat., Bot.*, sér. 7, **17**(5–6), 327.

Blockeel T. (2017) The *Ulota crispa* group in Britain and Ireland, with notes on other species of the genus, *Field Bryol.* **117**, 8.

Blockeel T., Turner J. (2013) Tales of the unexpected, no. 2: *Ulota calvescens* in the southern Pennines, *Field Bryol.* **110**, 35.

Bridel S. É. v. (1812) *Muscologia Recentiorum Supplementum 2.* C. G. Ettinger, Gotha, p. 257.

Bridel S. É. v. (1819) *Muscologia Recentiorum Supplementum 4.* C. G. Ettinger, Gotha, pp. 112–113.

Bridel S. É. v. (1826) *Bryologia Universa 1*. J. A. Barth, Leipzig, pp. 298–304.

Bridel S. É. v. (1827) *Bryologia Universa 1*. J. A. Barth, Leipzig, pp. 792–795.

Brotherus V. F. (1893) Some new species of Australian mosses. II, *Öfvers. Kongl. Vetensk.-Akad. Förh.* **35**, 34.

Brotherus V. F. (1929) Musci. In: Handel-Mazzetti H. F. von (Ed.), *Symbolae Sinicae*, pp. 70–71.

Bruch P. (1827) *Ulota crispula*. In: Bridel S. É. v. *Bryologia Universa 1*. J. A. Barth, Leipzig, pp. 747–856.

Bytebier B., Chuah-Petiot M. (2002) A preliminary checklist of the bryoflora of the Taita Hills, Kenya, *Trop. Bryol.* **22**, 55.

Calabrese G. M. (2006) A taxonomic revision of *Zygodon* (Orthotrichaceae) in southern South America, *Bryologist* **109**, 453.

Caparrós R., Lara F., Draper I., Mazimpaka V., Garilleti R. (2016) Integrative taxonomy sheds light on an old problem: The *Ulota crispa* complex (Orthotrichaceae, Musci), *Bot. J. Linn. Soc.* **180**, 427.

Caparrós R., Lara F., Long D. G., Mazimpaka V., Garilleti R. (2011) Two new species of *Ulota* (Orthotrichaceae, Bryopsida) with multicellular spores, from the Hengduan Mountains, Southwestern China, *J. Bryol.* **33**, 210.

Cardot J. (1905) Notice préliminaire sur les mousse recueillies par l'Expédition antarctique suédoise, *Bull. Herb. Boissier* **5**, 997.

Carrington B. (1862) *Ulota calvescens*. In: Rabenhorst G. L., *Bryotheca Europaea* **11**, p. 520.

Chikovani N., Svanidze T. (2004) Checklist of bryophyte species of Georgia, *Braun-Blanquetia* **34**, 97.

Crum H. A., Anderson L. E. (1981) *Ulota*. In: *Mosses of Eastern North America*. Vol. 2. Columbia University Press, New York, pp. 720–731.

Delogne C. H. (1884) [1885] *Flore Cryptogamique de la Belgique 2*. H. Manceaux, Bruxelles, pp. 115–338.

Dirkse G. M., Bouman A. C., Losada-Lima A. (1993) Bryophytes of the Canary Islands, an annotated checklist, *Cryptog. Bryol. Lichénol.* **14**, 1.

Dirkse G. M., Losada-Lima A. (2011) Additions and amendments to the moss flora of the Canary Islands, *Cryptog., Bryol.* **32**(1), 37.

Draper I., Garilleti R., Calleja J. A., Flagmeier M., Mazimpaka V., Vigalondo B., Lara F. (2021) Insights into the evolutionary history of the subfamily Orthotrichoideae (Orthotrichaceae, Bryophyta): New and former supra-specific taxa so far obscured by prevailing homoplasy, *Frontiers Pl. Sci.* **12**, 629035. https://doi.org/10.3389/fpls.2021.629035.

Draper I., Mazimpaka V., Albertos B., Garilleti R., Lara F. (2005) A survey of the epiphytic bryophyte flora of the Rif and Tazzeka Mountains (northern Morocco), *J. Bryol.* **27**, 23.

Draper I., Mazimpaka V., Lara F. (2008) New records to the epiphytic bryophyte flora of Tunisia, *Cryptog. Bryol.* **29**, 83.

Dusén P. (1903) Patagonian and Fuegian mosses. *Rep. Princeton Univ. Exp. Patagonia, Botany* **8**(3), 63.

El-Saadawi W., Badawi A., Shabbara H. M., Salama U. Y. A., Refai M. S. M. (1999) An updated list of Egyptian mosses, *Taeckholmia* **19**(2), 77.

Erzberger P. (2003) The number of stomata per sporophyte and its variability in the species of the *Ulota crispa* complex and *Ulota drummondii* (Musci, Orthotrichaceae), *Lindbergia* **2003**, 14.

Fedosov V. E., Ignatova E. A. (2018) On the genus *Ulota* (Orthotrichaceae, Bryophyta) in Russia, *Novosti Sist. Nizsh. Rast.* **52**(1), 141.

Fife A. J. (1995) Checklist of the mosses of New Zealand, *Bryologist* **98**, 313.

Fife A. J. (2017) Orthotrichaceae. In: Breitwieser I., Wilton A. D. *Fl. New Zealand – Mosses*. Fascicle 31. Manaaki Whenua Press, Lincoln. http://dx.doi.org/10.7931/B1J01C.

Gangulee H. C. (1976) *Mosses of Eastern India and Adjacent Regions 5*. Privately published, Calcutta.

Gao C. (Institute of Forestry and Pedalogy). (1977) *Flora Muscorum China Boreali-Orientalis*. Science Press, Beijing.

Garilleti R., Albertos B., Draper I., Calleja J. A., Mazimpaka V., Lara F. (2020) Two complex typifications and a new name to unravel *Ulota germana* sensu Malta non (Mont.) Mitt. (Orthotrichaceae), *Bryologist* **123**(2), 163.

Garilleti R., Albertos B., Draper I., Lara F. (2021) Updated description and distribution of the Patagonian moss *Ulota macrodontia* Dusén ex Malta (Orthotrichaceae), *J. Bryol.* https://doi.org/10.1080/03736687.2021.1934623.

Garilleti R., Lara F., Albertos B., Mazimpaka V. (2000) Peristomal ornamentation, a precise character for discrimination of *Ulota bruchii* and *U. crispa* (Bryopsida, Orthotrichaceae), *J. Bryol.* **22**, 273.

Garilleti R., Mazimpaka V., Lara F. (2012) New *Ulota* species with multicellular spores from southern South America, *Bryologist* **115**, 585.

Garilleti R., Mazimpaka V., Lara F. (2015) *Ulota larrainii* (Orthotrichoideae, Orthotrichaceae, Bryophyta) a new species from Chile, with comments on the worldwide diversification of the genus, *Phytotaxa* **217**, 133.

Garilleti R., Puelles L. M., Mazimpaka V., Lara F. (2016) A new lectotypification of *Ulota macrodontia* Dusén ex Malta (Orthotrichaceae, Bryophyta), *J. Bryol.* **38**(4), 355.

Germishuizen G., Meyer N. L. (2003) Plants of southern Africa: An annotated checklist. *Strelitzia* **14**.

Ghahreman A., Faridi M., Shirzadian S., Attar F. (2007) New and interesting moss records for Iran, *Türk Bot. Derg.* **31**, 41.

Goffinet B., Shaw A. J., Cox C. J., Wickett N. J., Boles S. B. (2004) Phylogenetic inferences in the Orthotrichoideae (Orthotrichaceae, Bryophyta) based on variation in four loci from all genomes, *Monogr. Syst. Bot. Missouri Bot. Gard.* **98**, 270.

Goffinet B., Vitt D. H. (1998) Revised generic classification of the Orthotrichaceae based on a molecular phylogeny and comparative morphology. In: *Bryology for the Twenty-first Century.* Maney Publishing and the British Bryological Society, Leeds, pp. 143–159.

Grout A. J. (1935) *Ulota.* In: *Moss flora of North America north of Mexico, vol. 2.* The Author, Newfane, Vermont, pp. 131–138.

Grout A. J. (1946) *Ulota.* In: Britton N. L. (Ed.), *North American Flora, 15A.* New York Botanical Garden, Bronx, New York, pp. 25–29.

Guo S.-L., Cao T., Tan B. C. (2007a) Three new species records of Orthotrichaceae (Bryopsida) in China, with comments on their type specimens, *Cryptog. Bryol.* **28**, 149.

Guo S.-L., Enroth J., Koponen T. (2007b) Bryophyte flora of Hunan province, China. – Orthotrichaceae, *Ann. Bot. Fenn.* **44**, 1.

Guo S.-L., Enroth J., Virtanen V. (2004) Bryophyte flora of Hunan Province, China. 10. *Ulota gymnostoma* sp. nova (Orthotrichaceae), *Ann. Bot. Fenn.* **41**, 459.

Guo S.-L., Zhen Y.-Y., Cao T., He S. (2010) New synonym and record of the genus *Ulota* D. Mohr (Musci, Orthotrichaceae) in moss flora of China, *Acta Bryolichenol. Asiat.* **3**, 51.

Hedderson T. A. J., Bizuru E., Mujawamariya M., Raondry-Rakotoarisoa N. (2014) New and additional moss records for Rwanda, *J. Bryol.* **36**(1), 72.

Hedwig J. (1801) *Species Muscorum Frondosorum.* Joannis Ambrosii Barthii, Lipsiae.

Heegaard E., Hangelbroek H. H. (1999) The distribution of *Ulota crispa* at a local scale in relation to both dispersal-and habitat-related factors, *Lindbergia* **24**, 65.

Héribaud J. (1899) Les muscinées d'Auvergne. *Mém. Acad. Sci. Clermont-Ferrand,* sér. 2 **14**.

Heyn C. C., Herrnstadt I. (2004) *The bryophyte flora of Israel and adjacent regions.* The Israel Academy of Sciences and Humanities, Jerusalem.

Hoe W. J., Crum H. A. (1971) [1972] Three new moss species from the Hawaiian Islands, *Bryologist* **74**, 484.

Holyoak D. T. (2002) *Ulota calvescens* with hairy calyptrae, *Bull. Brit. Bryol. Soc.* **79**, 59.

Hong W. S., Ando H. (1959) An enumeration of mosses recorded from Korea, with some new additions to the Korean flora, *Theses Catholic Med. Coll.* **3**, 371.

Hornschuch C. F. (1827) *Ulota bruchii.* In: Bridel S. É. v. *Bryologia Universa 1.* J. A. Barth, Leipzig, pp. 747–856.

Hornschuch C. F. (1841) Muscorum frondosorum novorum, quos in Africa australiori collegerunt Ecklon, Drège, Mundt et Maire, descriptiones, *Linnaea* **15**, 113.

Hooker J. D. (1867) *Handbook of the New Zealand Flora 2*. Reeve & Co., London, pp. 393–798.

Hooker J. D., Wilson W. (1847) Musci. (En Hooker, J. D. The botany of the Antarctic Voyage of H. M. Discovery ships Erebus and Terror, in the years 1839–1843 under the command of Captain Sir James Clark Ross). I. *Flora Antarctica*, Part II: 209–574, pls. 81–198. Reeve & Son, London.

Hooker J. D., Wilson W. (1860) Musci. (En Hooker, J. D. The botany of the Antarctic Voyage of H. M. Discovery ships Erebus and Terror, in the years 1839–1843 under the command of Captain Sir James Clark Ross). II. *Flora Tasmaniae*, Part III: 184.

Hooker W. J., Greville R. K. (1824) Art. XXIII. Sketch of the characters of the species of mosses, belonging to the genera *Orthotrichum* (including *Schlotheimia*, *Micromitrion* and *Ulota*), *Glyphomitrium*, and *Zygodon*, *Edinburgh J. Sci.* **1**, 110.

Ignatov M. S., Ochyra R. (1994) Bryophytes of Altai Mountains. III. The genus *Ulota* (Orthotrichaceae, Musci), *Arctoa* **3**, 59.

Intergovernmental Panel on Climate Change (IPCC). (2006) IPCC Guidelines for National Greenhouse Gas Inventories. Volume 4. Egglestone H. S., Buendia L., Miwa K., Ngara T., Tanabe K. (Eds), *Intergovernmental Panel on Climate Change (IPCC), IPCC/IGES*, Hayama, Japan. http://www.ipcc-nggip.iges.or.jp/public/2006gl/vol4.html.

Ireland R. R. Jr. (1982) *Moss flora of the Maritime Provinces. No. 13*. Publications in Botany, Ottawa, pp. 401–406.

Iwatsuki Z. (1959) A revision of the Japanese species of the genus *Ulota*, *J. Hattori Bot. Lab.* **21**, 138.

Iwatsuki Z. (1969) Bryological miscellanies XIX–XX, *J. Hattori Bot. Lab.* **32**, 269.

Iwatsuki Z. (1991) *Catalog of the mosses of Japan*. Hattori Botanical Laboratory, Nichinan.

Jaeger A. (1874) Adumbratio florae muscorum totius orbis terrarium. Part 4. *Ber. Thätigk. St. Gallischen Naturwiss. Ges.* **1872–1873**, 61.

Jaeger A., Sauerbeck F. (1880) Adumbratio flore muscorum totius orbis terrarum. Part 9. *Ber. Thätigk. St. Gallischen Naturwiss. Ges.* **1877–1878**, 257.

Juratzka J. (1864) *Ulota rehmanni* n. sp. *Verh. K.K. Zool.-Bot. Ges. Wien* **14**, 191.

Keller B. A. (1914) Through valleys and mountains of Altai. Trudy Poczv.-Bot. Expedizij po Issled. Kolonizazionnykh rajonov Aziatskoi Rossi. Pt. 2. Bot. Issled. 1910 goda **6**, 1.

Kindberg N. C. (1883) Die Arten der Laubmoose (Bryineae) Schwedens und Norwegens. *Bih. Kongl. Svenska Vetensk.-Akad. Handl.* **7**(9), 1.

Kindberg N. C. (1888) *Enumeratio Bryinearum Exoticarum*. Officina Corresp. Ostrogoth., Linkoeping, pp. 1–83.

Kindberg N. C. (1889) *Enumeratio Bryinearum Exoticarum, Supplementum 1*. Officina Corresp. Ostrogoth., Linkoeping, pp. 85–96.

Kindberg N. C. (1890) *Orthotrichum connectens*. In: Macoun J., List of mosses collected in the neighborhood of Ottawa. *Ottawa Naturalist* **3**, pp. 149–152.

Kindberg N. C. (1891) *Enumeratio Bryinearum Exoticarum, supplementum 2*. Officina Corresp. Ostrogoth., Linkoeping, pp. 97–108.

Kindberg N. C. (1897) Part 2. Acrocarpous. In: Kindberg N. C. (Ed.), *European and North American Bryineae (Mosses)*. Linköpings Lithografiska, Linköping, pp. 153–410.

Köckinger H., Schröck C., Krisai, R., Zechmeister H. G. (2012) *Checklist of Austrian Bryophytes* (http://131.130.59.133/projekte/moose/). Acceded the 03/04/2012.

Kürschner H., Parolly G. (1998) Lebensstrategien stammepiphytischer moose in regenwaldern am andenostabhang und im Amazonas-Tiefland von nord-Peru. [Life strategies of epiphytic bryophyte vegetation in rainforests along the eastern Andean slopes and the Amazon lowlands of northern Peru], *Nova Hedwigia* **67**, 1.

Lara F., Garilleti R., Goffinet B., Draper I., Medina R., Vigalondo E., Mazimpaka V. (2016) *Lewinskya*, a new genus to accommodate the phaneroporous and monoicous taxa of *Orthotrichum* (Bryophyta, Orthotrichaceae), *Cryptog. Bryol.* **37**, 361.

Lara F., Garilleti R., Mazimpaka V., Guerra J. (2014) Orthotrichaceae 5, 15–17. In: Guerra J., Cros R. M. (Coordinadores), *Flora Briofítica Ibérica*. Sociedad Española de Briología, Murcia.

Lara F., Mazimpaka V., Medina R., Caparrós R., Garilleti R. (2010) Northeastern Turkey, an unnoticed but very important area for the Orthotrichaceae (Bryophyta), *Nova Hedwigia Beih.* **138**, 165.

Lewinsky J. (1977) The genus *Orthotrichum*, morphological studies and evolutionary remarks, *J. Hattori Bot. Lab.* **43**, 31.

Lewinsky J. (1993) A synopsis of the genus *Orthotrichum* Hedw. (Musci, Orthotrichaceae), *Bryobrothera* **2**, 1.

Lindberg S. O. (1879) *Musci Scandinavici.* Officina Iesaiae, Upsala.

Magill R. E., van Rooy J. (1998) *Ulota.* In: *Flora of Southern Africa, Bryophyta. Part 1 Musci, Fascicle 3 Erpodiaceae–Hookeriaceae.* Botanical Research Institute, Pretoria, pp. 504–505.

Malta N. (1927) Die Ulota-Arten Süd-Amerikas, *Acta Horti Bot. Univ. Latv.* **2**, 165.

Malta N. (1933) A survey of the Australasian species of *Ulota*, *Acta Horti Bot. Univ. Latv.* **7**, 1.

Mamtimin S., Wu P.-C., Deguchi H. (2004) New records of the mosses in Xinjiang, China, *Acta Bot. Yunnan.* **26**, 19.

Marline L., Andriamiarisoa R. L., Bardat J., Chuah-Petiot M. S., Hedderson T. A. J., Reeb C., Strasberg D., Wilding N., Ah-Peng C. (2012) Checklist of the bryophytes of Madagascar, *Cryptog. Bryol.* **33**(3), 199.

Martincic A. (2003) List of the Slovenian mosses, *Hacquetia* **2**(1), 91.

Mitten W. (1859) Descriptions of some new species of Musci from New Zealand and other parts of the Southern Hemisphere, together with an enumeration of the species collected in Tasmania by William Archer, arranged upon the plan proposed in the Musci Indiae Orientalis, *J. Proc. Linn. Soc., Bot.* **4**, 64.

Mitten W. (1864a) The "Bryologia" of the survey of the 49th parallel of latitude, *J. Proc. Linn. Soc., Bot.* **8**, 12.

Mitten W. (1864b) Contributions to the cryptogamic flora of the Atlantic Islands, *J. Proc. Linn. Soc., Bot.* **8**, 1.

Mitten W. (1869) Musci Austro-Americani enumeratio muscorum omnium Austroamericanorum auctori hucusque cognitorum, *J. Linn. Soc., Bot.* **12**, 189.

Mitten W. (1870) Musci. In: Godman F. D. C. (Ed.), *Natural history of the Azores, or Western Islands.* John Van Voorst, London, pp. 288–316.

Mitten W. (1891) An enumeration of all the species of Musci and Hepaticae recorded from Japan, *Trans. Linn. Soc. London, Bot.* **3**, 153.

Mohr D. M. H. (1806) Observations on *Orthotrichum* and *Neckera*, together with some other genera of mosses, *Ann. Bot. (König & Sims)* **2**, 532.

Montagne J. F. C. (1843) Quatrième centurie de plantes cellulaires exotiques nouvelles, decades I–VI, *Ann. Sci. Nat. Bot.* (*sér. 2*) **19**, 238.

Montagne J. F. C. (1845) Cinquième centurie de plantes cellulaires exotiques nouvelles, décades I–VI, *Ann. Sci. Nat. Bot.* (*sér. 3*) **4**, 86.

Müller C. (1845) Beiträge zu einer Flora der Aequinoctial-Gegenden, *Laubmoose, Linnaea* **18**, 667.

Müller C. (1862) Additamenta ad synopsin muscorum nova, *Bot. Zeitung (Berlin)* **20**, 348.

Müller C. (1883) Die auf der Expedition S. M. S. "Gazelle" von Dr. Naumann gesammelten Laubmoose. *Bot. Jahrb. Syst.* **5**, 76.

Müller C. (1885) Bryologia Fuegiana, *Flora* **68**, 391.

Müller C. (1897) Prodromus bryologiae Argentinicae atque regionum vicinarum III, *Hedwigia* **36**, 84.

Müller C., Kindberg N. C. (1892) *Ulota obtusiuscula.* In: Macoun J., Kindberg N. C. *Catalogue of Canadian Plants, Part VI, Musci.* William Foster Brown & Co., Montreal, pp. 82–85.

Muñoz-Puelles L., Lara F., Mazimpaka V., Garilleti R. (2017) Vindication of *Ulota pygmaeothecia* (Orthotrichaceae, Bryophyta), *Phytotaxa* **317**(3), 161.

Nakanishi S. (1963) A record of travels in Taiwan, *Hikobia* **3**, 316.

Natcheva R., Ganeva A. (2005) Check-list of the bryophytes of Bulgaria. II. Musci, *Cryptog. Bryol.* **26**, 209.

Noguchi A. (1937) Studies on the Japanese mosses of the orders Isobryales and Hookeriales II, *J. Sci. Hiroshima Univ., Ser. B, Div. 2* (*Bot.*) **3**, 37.

Noguchi A. (1939) Studies on the Japanese mosses of the orders Isobryales and Hookeriales IV, *J. Sci. Hiroshima Univ., Ser. B, Div. 2 (Bot.)* **3**, 211.

Noguchi A., Iwatsuki Z. (1989) *Illustrated Moss Flora of Japan: Part 3.* Hattori Botanical Laboratory, Nichinan.

Nyholm E. (1960) *Ulota.* In: *Illustrated Moss Flora of Fennoscandia. II. Musci. Fasc. 2.* Swedish Natural Science Research Council, Stockholm, pp. 315–321.

Nyholm E. (1998) Orthotrichaceae. In: *Illustrated Flora of Nordic Mosses. Fasc. 4.* Nordic Bryological Society, Copenhagen & Lund.

Ochi H. (1972) A revision of African Bryoideae, Musci (First part), *J. Fac. Educ. Tottori Univ., Nat. Sci.* **23**, 1.

Ochi H. (1973) A revision of African Bryoideae, Musci (Second part), *J. Fac. Educ. Tottori Univ., Nat. Sci.* **24**, 23.

O'Shea B. J. (1997) The mosses of sub-Saharan Africa 1. A review of taxonomic progress, *J. Bryol.* **19**, 509.

O'Shea B. J. (1999) Checklist of the mosses of sub-Saharan Africa (version 3, 11/99), *Trop. Bryol. Res. Rep.* **1**, 1.

O'Shea B. J. (2006) Checklist of the mosses of sub-Saharan Africa (version 5, 12/06), *Trop. Bryol. Res. Rep.* **6**, 1.

O'Shea B. J. (2008) Name changes for 13 African mosses with invalid names, *Trop. Bryol.* **29**, 4.

Palisot de Beauvois A. M. F. J. (1805) *Prodrome des Cinquième et Sixième Familles de l'Aethéogamie.* Pournier Fils, Paris.

Paris J. É. G. N. (1906) *Index Bryologicus* (ed. 2). Published by the Author, Genéve.

Piré L., Cardot J. (1885) Les muscinées des environs de Spa, *Bull. Soc. Roy. Bot. Belgique* **24**, 326.

Plášek V., Sawicki J., Ochyra R., Szczecińska M., Kulik T. (2015) New taxonomical arrangement of the traditionally conceived genera *Orthotrichum* and *Ulota* (Orthotrichaceae, Bryophyta), *Acta Mus. Siles. Sci. Nat.* **64**, 169.

Plášek V., Smoczyk M., Ochyra R. (2016) Rediscovery of the epiphytic moss *Ulota coarctata* (Orthotrichaceae) in Poland, *Polish Bot. J.* **61**, 99.

Pócs T., Lye K. (1999) New records and additions to the hepatic flora of Uganda. 2, *Trop. Bryol.* **17**, 23.

Potier de la Varde R. (1955) Mousses récoltées par M. le Dr. Olov Hedberg, en Afrique orientale, au cours de la mission suédoise de 1948, *Ark. Bot., n.s.* **3**, 125.

Preston C. D. (1984) A check-list of Greek mosses, *J. Bryol.* **13**, 43.

Privitera M., Aleffi M., Bertani G., *et al.* (2010) Survey of the bryophyte diversity of the Carnic Alps, including some interesting records for the Italian bryoflora, *Fl. Medit.* **20**, 193.

Ramsay H. P. (2006) *Ulota.* In: *Flora of Australia. Vol. 51. Mosses 1.* Australian Biological Research Studies, Canberra, pp. 228–236.

Ramsay H. P., Cairns A., Meagher D. (2017) *Macromitrium erythrocomum* (Bryophyta: Orthotrichaceae), a new species from tropical Queensland, Australia, *Telopea* **20**, 261.

Rodway L. (1912) Tasmanian Bryophyta, *Pap. & Proc. Roy. Soc. Tasmania* **1912**, 3.

Ros R. M., Cano M. J., Guerra J. (1999) Bryophyte checklist of Northern Africa, *J. Bryol.* **21**, 207.

Ros R. M., Mazimpaka V., Abou-Salama U.Y., *et al.* (2013) Mosses of the Mediterranean, an annotated checklist, *Cryptog. Bryol.* **34**(2), 99.

Rosman-Hartog N., Touw A. (1987) On the taxonomic status of *Ulota bruchii* Hornsch. ex Brid., *U. crispa* (Hedw.) Brid. and *U. crispula* Bruch ex Brid, *Lindbergia* **13**, 159.

Rykovsky G., Maslovsky O. (2004) *Flora of Belarus Bryophyta. Vol. 1. Andreaeaopsida-Bryopsida.* Technalohija, Minsk.

Sabovljević M. S. (2006) Checklist of mosses of Croatia, *Arch. Biol. Sci. (Belgrade)* **58**, 45.

Sainsbury G. O. K. (1945) New and critical species of New Zealand mosses, *Trans. Roy. Soc. New Zealand* **75**, 169.

Sainsbury G. O. K. (1955) A handbook of the New Zealand mosses, *Bull. Roy. Soc. New Zealand* **5**, 217.

Sainsbury G. O. K., Allison K. W. (1962) Mosses from the Auckland Islands and Campbell Island, *Rec. Domin. Mus.* **4**, 133.

Sakurai K. (1935) Beobachtungen über japanische Moosflora. VII. *Bot. Mag. (Tokyo)* **49**, 126.

Schimper W. P. (1876) *Synopsis Muscorum Europaeorum* (ed. 2). E. Schweizerbart, Stuttgardt.

Seppelt R. D. (1978) Studies on the bryoflora of Macquarie Island II. *Ulota phyllantha* Brid, *New Zealand J. Bot.* **16**, 21.

Siebel H. N., During H. J. (2006) *Beknopte Mosflora van Nederland en België.* KNNV Uitgeverij, Utrecht.

Smith A. J. E. (1978) *Ulota.* In: *The moss flora of Britain and Ireland* (ed. 1). Cambridge University Press, Cambridge, pp. 486–491.

Smith A. J. E. (2004) *The moss flora of Britain and Ireland* (ed. 2). Cambridge University Press, Cambridge.

Smith A. J. E., Hill M. O. (1975) A taxonomic investigation of *Ulota bruchii* Hornsch. ex Brid., *U. crispa* (Hedw.) Brid. and *U. crispula* Bruch ex Brid. European material, *J. Bryol.* **8**, 423.

Smith A. J. E., Proctor M. C. F. (1993) Further observations on the *Ulota crispa* complex, *J. Hattori Bot. Lab.* **74**, 171.

Smith J. E. (1813) *English Botany* **36**, pl. 2521–2592. Author, London.

Streimann H., Curnow J. (1989) Catalogue of mosses of Australia and its external territories, *Austral. Fl. Fauna* **10**, 388.

Streimann H., Klazenga N. (2002) Catalogue of Australian mosses, *Fl. Australia Suppl.* **17**, 181.

Sullivant W. S. (1874) *Icones Muscorum, Supplement viii.* Charles W. Sever/Trüber, Cambridge, Mass./London.

Suzuki T., Iwatsuki Z. (2011) Four newly recorded species of Orthotrichaceae (Musci) from Japan, *Hattoria* **2**, 35.

Suzuki T., Iwatsuki Z. (2013) Notes on *Ulota* in Japan, *Hattoria* **4**, 99.

Sotiaux A., Pioli A., Royaud A., Schumacker R., Vanderpoorten A. (2007) A checklist of the bryophytes of Corsica (France): New records and a review of the literature, *J. Bryol.* **29**, 41.

Sotiaux A., Sotiaux O. (1999) *Ulota rehmannii* Jur. (Orthotrichaceae, Musci) nouveau pour la bryoflore belge dans le massif ardennais, *Belg. J. Bot.* **132**(2), 153.

Turland N. J., Wiersema J. H., Barrie F. R., *et al.* (Eds.) (2018) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017.* Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten.

van der Wijk R., Margadant W. D., Florschütz P. A. (1969) Index Muscorum. 5 (T–Z, Appendix), *Regnum Veg.* **65**.

van Rooy J., Wyk A. E. v. (1992) A conspectus of the subfamily Macromitrioideae (Bryopsida: Orthotrichaceae) in southern Africa, *Bryologist* **95**, 205.

Venturi G. (1890) *Ulota megalospora.* In: Röll J. Vorläufige Mittheilungen über die von in Jahr 1888 in Nord-Amerika Gesammelten Neuen Arten und Variatäten der Laubmoose, *Bot. Centralbl.* **44**(12), pp. 385–391.

Vitt D. H. (1970) *The family Orthotrichaceae (Musci) in North America, north of Mexico.* [Ph.D. dissertation.]. University of Michigan, Ann Arbor.

Vitt D. H. (1971) The infrageneric evolution, phylogeny, and taxonomy of the genus *Orthotrichum* (Musci) in North America, *Nova Hedwigia* **21**, 683.

Vitt D. H. (1974) A key and synopsis of the mosses of Campbell Island, New Zealand, *New Zealand J. Bot.* **12**, 185.

Vitt D. H. (1979) The moss flora of the Auckland Islands, New Zealand, with a consideration of habitats, origins, and adaptations, *Canad. J. Bot.* **57**, 2226.

Vitt D. H. (1993) Bryophyte flora of the Huon Peninsula, Papua New Guinea. LIII, *Acta Bot. Fenn.* **148**, 5.

Vitt D. H. (2003) *Ulota.* In: *Bryophyte Flora of North America, Provisional Publication.* http://www.mobot.org/plantscience/bfna/V2/OrthUlota.htm.

Vitt D. H. (2014) Orthotrichaceae. In: *Flora of North America North of Mexico*, Vol. 28. Oxford University Press, New York, pp. 37–82.

Wahlenberg G. (1812) *Flora Lapponica* (Wahlenberg). Taberna Libraria Scholae, Berlin.

Wang Q.-H., Dong S.-S., Zhang J.-L., Liu Y., Jia Y. (2021) Phylogeny of *Orthotrichum* s.l. and *Ulota* s.l. (Orthotrichaceae, Bryophyta): Insights into stomatal evolution, *J. Syst. Evol.* https://doi.org/10.1111/jse.12713.

Wang Q.-H., Jia Y. (2012a) A taxonomic revision of the Asian species of *Ulota* Mohr (Orthotrichaceae), *Bryologist* **115**, 412.

Wang Q.-H., Jia Y. (2012b) Three new synonyms of *Ulota crispa* (Hedw.) Brid. (Orthotrichaceae, Bryopsida), *J. Bryol.* **34**(4), 303.

Wang Q.-H., Jia Y. (2014) Taxonomic status of *Ulota tanganyikae* P. de la Varde (Orthotrichaceae, Bryopsida) from Africa, *J. Bryol.* **36**(1), 78.

Wang Q.-H., Jia Y. (2016) A taxonomic revision of *Ulota* Mohr (Orthotrichaceae) in South and Central America, *Pl. Diversity* **38**, 82.

Wang Q.-H., Jia Y. (2018a) Rediscovery of *Ulota germana* (Mont.) Mitt. in New Zealand (Orthotrichaceae), *Bull. Bot. Res., Harbin* **38**(1), 1.

Wang Q.-H., Jia Y. (2018b) *Ulota panchengiana*, a new species from China and notes on the taxonomy of *U. morrisonensis* Horik. & Nog. (Orthotrichaceae), *Cryptog., Bryol.* **39**(4), 467.

Weymouth W. A. (1893) Some additions to the moss flora of Tasmania, *Pap. Proc. & Rep. Roy. Soc. Tasmania*, pp. 200–210.

Wigginton M. J. (2002) Checklist and distribution of the liverworts and hornworts of sub-Saharan Africa, including the East African islands, *Trop. Bryol. Res. Rep.* **3**, 1.

Wigginton M. J., Porley R. D., Hodgetts N. G. (1999) Bryophytes of Uganda. 1. BBS Tropical Bryology Group expeditions, 1996–1998. Introduction and collecting sites, *Trop. Bryol.* **16**, 165.

Wilbraham J. (2008) Bryophyte flora of Uganda. 8. Orthotrichaceae Part 1 – Macromitrioideae, *J. Bryol.* **30**, 201.

Worley I. A., Iwatsuki Z. (1970) A checklist of the mosses of Alaska, *Bryologist* **73**, 59.

Index to Scientific Names

A
Atlantichella, 58, 287
Atlantichella calvescens, 1

B
Bryodixonia, 34
Bryodixonia perichaetialis, 6, 217
Bryum striatum, 71

G
Groutiella, 3

L
Leptodontium viticulosoides, 32
Lewinskya, 34, 287

M
Macromitrium, 120
Macromitrium drummondii, 103
Macromitrium erythrocomum, 32

N
Neckera ulophylla, 71
Nyholmiella, 34

O
O. americanum, 8
O. erubescens, 210
O. striatum, 3
Orthotrichum, 1, 34, 170, 179, 187, 289, 280
Orthotrichum americanum, 138
Orthotrichum anomalum, 3
Orthotrichum anomalum var. *americanum*, 138
Orthotrichum bicolor, 281
Orthotrichum brevicolle, 126
Orthotrichum carinatum, 117
Orthotrichum chilense, 126
Orthotrichum cirratum, 92
Orthotrichum clausum, 61
Orthotrichum clavatum, 61
Orthotrichum coarctatum, 8, 61
Orthotrichum consobrinum, 150
Orthotrichum crispulum, 86
Orthotrichum crispum, 3, 6, 71
Orthotrichum crispum subsp. *crispulum*, 86
Orthotrichum crispum var. *brevifolium*, 139
Orthotrichum crispum var. *curvifolium*, 92
Orthotrichum crispum var. *macrocarpon*, 92
Orthotrichum crispum var. *minus*, 93
Orthotrichum cupulatum var. *crispulum*, 87
Orthotrichum curvifolium, 6, 92
Orthotrichum dilatatum, 71
Orthotrichum drummondii, 6, 103
Orthotrichum eremitense, 117
Orthotrichum fasciculare, 221
Orthotrichum fulvellum, 163
Orthotrichum germanum, 126
Orthotrichum hookeri, 250
Orthotrichum hudchinsianum, 139
Orthotrichum hutchinsiae, 6, 138
Orthotrichum hutchinsiae var. *nigrescens*, 139
Orthotrichum japonicum, 149
Orthotrichum jetteae, 159
Orthotrichum jutlandicum, 221, 280
Orthotrichum laureri, 92
Orthotrichum lobbianum, 126
Orthotrichum ludwigii, 6
Orthotrichum luteolum, 162

Orthotrichum luteum, 6, 72
Orthotrichum lyellii, 58
Orthotrichum macrocalycinum, 169
Orthotrichum marginatum, 170
Orthotrichum maritimum, 221
Orthotrichum nicholsonii, 92
Orthotrichum nigricans, 139
Orthotrichum obtusiusculum, 204
Orthotrichum phyllanthoides, 9, 279
Orthotrichum phyllanthum, 221
Orthotrichum plicatum, 61
Orthotrichum pygmaeothecium, 163
Orthotrichum pyriforme, 71
Orthotrichum rehmannii, 235
Orthotrichum rhytiore, 245
Orthotrichum rufulum, 126
Orthotrichum saxatile var. *americanum*, 138
Orthotrichum scabridum, 92
Orthotrichum schmidii, 280
Orthotrichum schofieldii, 210
Orthotrichum strictum, 93, 139
Orthotrichum subrepens, 103
Orthotrichum subulatum, 186
Orthotrichum tasmanicum, 156, 267
Orthotrichum ulophyllum, 71
Orthotrichum ulophyllum ssp. *intermedium*, 146
Orthotrichum ulophyllum subsp. *Crispulum*, 86
Orthotrichum ulophyllum var. *intermedium*, 145

P
Plenogemma, 223, 287
Plenogemma phyllantha, 1
Ptychomitrium, 34
Pulvigera, 34, 287

S
Schlotheimia, 3

U
U. anceps, 6
U. angusti-limbata, 253, 283, 289
U. barclayi, 13, 18, 215, 289
U. bellii, 6
U. bellissima, 5
U. billbuckii, 28, 170, 251, 264, 270, 289
U. breviseta, 6
U. bruchii, 283, 289
U. calvescens, 74, 287, 289
U. coarctata, 13, 18, 19, 22, 28, 104, 271, 289
U. cochleata, 6, 19, 28, 284, 289
U. crispa, 5–7, 9, 54, 58, 70, 100, 104, 127, 146, 153, 161, 196, 218, 240, 285, 289
U. crispula, 4, 6, 147, 196, 289
U. curvifolia, 13, 28, 140, 166, 192, 284, 289
U. delicata, 5, 22, 28, 31, 104, 192, 289
U. dixonii, 6
U. drummondii, 4, 13, 19, 22, 25, 28, 31, 47, 54, 62, 100, 150, 205, 264, 271, 289
U. ecklonii, 24, 31, 284, 289
U. eurystoma, 5, 12, 18, 19, 22, 24, 54, 270, 289
U. fuegiana, 11, 28, 31, 127, 289
U. fulva, 6, 7
U. germana, 74, 289
U. gigantospora, 13, 188, 200, 270, 275, 283, 289
U. gymnostoma, 15, 18, 19, 22, 100, 215, 289
U. hattorii, 5
U. hutchinsiae, 8, 13, 17, 30, 93, 94, 104, 171, 284, 289
U. intermedia, 74, 196, 289
U. japonica, 13, 17, 31, 215, 236, 279, 289
U. larrainii, 9, 51, 179, 283, 289
U. laticiliata, 6, 284, 289
U. latisegmenta, 5, 21, 28, 100, 210, 251, 283, 289
U. longifolia, 5
U. lutea, 6, 157
U. luteola, 6, 13, 17, 179, 283, 289
U. macrocalycina, 13, 48, 188, 210, 241, 289
U. macrocarpa, 5
U. macrodontia, 28, 183, 230, 232, 289
U. magellanica, 13, 17, 28, 51, 170, 192, 229, 236, 251, 268, 289
U. maltiana, 9, 283, 289
U. megalospora, 5, 11, 13, 15, 17, 19, 21, 28, 30, 47, 166, 241, 268, 289
U. membranata, 6, 13, 18, 28, 131, 251, 270, 289
U. morrisonensis, 28, 183, 200, 283, 289
U. nipponensis, 5
U. novae-seelandiae, 6
U. novo-guinensis, 28, 30, 31, 46, 130, 223, 270, 283, 289
U. obtusiuscula, 19, 21, 74, 116, 158, 283, 289
U. orientalis, 5
U. pacifica, 5
U. panchengiana, 5, 19, 289
U. perbreviseta, 18, 19, 152, 218, 289
U. perichaetialis, 15, 18, 22, 28, 31, 271, 289
U. phyllantha, 6, 17, 30, 104, 283, 284, 285, 287, 289
U. pusilla, 13, 17, 19, 171, 230, 289
U. pycnophylla, 12, 13, 17, 165, 171, 289
U. pygmaeothecia, 6
U. rehmannii, 5, 7, 13, 24, 31, 116, 236, 244, 268, 279, 289
U. reptans, 4, 13, 15, 19, 116, 166, 238, 268, 289
U. rhytiore, 12, 18, 19, 22, 135, 210, 215, 218, 289
U. robusta, 4, 5, 19, 28, 116, 283, 289
U. rubella, 6, 12, 45, 283, 289
U. rufula, 6

U. schmidii, 4
U. splendida, 6, 13, 21, 223, 253, 283, 289
U. streptodon, 9, 13, 19, 22, 28, 30, 31, 270, 283, 289
U. tanganyikae, 7
U. viridis, 6, 13, 31, 69, 156, 268, 289
U. weymouthii, 6
U. yakushimensis, 5, 18, 22, 28, 30, 31, 54, 289
U. yunnanensis, 5, 24, 46, 131, 236, 270, 283, 289
Ulota, 1
Ulota alaskana, 204
Ulota americana, 93, 139
Ulota anceps, 265
Ulota angusti-limbata, 6, 17, 42, 192
Ulota angustissima, 117
Ulota appressa, 265
Ulota aurantiaca, 233
Ulota barclayi, 13, 17, 47, 171, 187
Ulota bellii, 71
Ulota bellii var. *longicolla*, 71
Ulota bellissima, 247
Ulota bicolor, 103
Ulota billbuckii, 9, 28, 50, 154, 179
Ulota brevicollis, 126
Ulota breviseta, 71
Ulota bruchii, 6, 19, 53, 73
Ulota calvescens, 7, 9, 15, 24, 57
Ulota camptopoda, 72
Ulota carinata, 117
Ulota cervina, 9, 72
Ulota chilensis, 126
Ulota cirrata, 93
Ulota coarctata, 6, 8, 22, 61
Ulota cochleata, 67, 123, 156, 210
Ulota connectens, 72
Ulota crispa, 5, 6, 11, 28, 47, 71, 88, 135, 150, 157, 166, 183, 192, 205, 222, 267
Ulota crispa ssp. *intermedia*, 146
Ulota crispa subsp. *crispula*, 87
Ulota crispa var. *alaskana*, 204
Ulota crispa var. *crispula*, 86
Ulota crispa var. *intermedia*, 145
Ulota crispa var. *microcarpa*, 93
Ulota crispa var. *minus*, 93
Ulota crispa var. *norvegica*, 72
Ulota crispula, 73, 86
Ulota crispula var. *dolosa*, 72
Ulota curvifolia, 6, 24, 92
Ulota darwinii, 118
Ulota delicata, 5, 19, 99, 159, 230
Ulota dixonii, 6, 265, 268
Ulota drummondii, 6, 103
Ulota ecklonii, 7, 109
Ulota eremitensis, 117
Ulota eurystoma, 12, 28, 31, 32, 112, 116
Ulota fernandeziana, 118
Ulota fuegiana, 70, 117
Ulota fuegiana subsp. *darwinii*, 118
Ulota fuegiana var. *crispata*, 118
Ulota fulva, 6, 7, 72
Ulota fulvella, 163
Ulota funstonii, 103
Ulota germana, 15, 126, 218
Ulota germana var. *breviseta*, 182
Ulota gigantospora, 5, 130, 241
Ulota glabella, 118, 121
Ulota gymnostoma, 135, 246
Ulota hamata, 178
Ulota hattorii, 257
Ulota hermitei, 118, 121
Ulota hutchinsiae, 6, 31, 138
Ulota immarginata, 163
Ulota intermedia, 5, 7, 145, 236
Ulota japonica, 4, 48, 149
Ulota japonica var. *perbreviseta*, 213
Ulota japonica var. *stenocarpa*, 103
Ulota jutlandica, 221
Ulota larrainii, 154
Ulota laticiliata, 155
Ulota latisegmenta, 159
Ulota lativentrosa, 229
Ulota lobbiana, 126
Ulota longifolia, 72
Ulota ludwigii, 61
Ulota lutea, 69, 72, 73
Ulota luteola, 162
Ulota macrocalycina, 13, 17, 21, 169, 179, 229, 235
Ulota macrocarpa, 5, 72
Ulota macrodontia, 12, 22, 28, 174
Ulota magellanica, 30, 178, 281
Ulota maltiana, 182
Ulota marginata, 170
Ulota maritima, 221
Ulota megalospora, 186
Ulota membranacea, 265
Ulota membranata, 30, 191
Ulota morrisonensis, 5, 195
Ulota nicholsonii, 92
Ulota nigricans, 139
Ulota nipponensis, 4, 149
Ulota nothofagi, 170
Ulota novae-seelandiae, 6, 265
Ulota novo-guinensis, 6, 31, 199
Ulota obtusiuscula, 19, 46, 204, 260
Ulota orientalis, 278
Ulota pacifica, 279
Ulota paivana, 57
Ulota panchengiana, 5, 20, 209
Ulota perbreviseta, 213
Ulota perichaetialis, 12, 217

Ulota persubulata, 126
Ulota phyllantha, 1, 18, 28, 221
Ulota phyllanthoides, 9, 279
Ulota pusilla, 175, 229
Ulota pycnophylla, 233
Ulota pygmaeothecia, 163, 164
Ulota rehmannii, 187, 235
Ulota reptans, 187, 240
Ulota rhytiore, 11, 13, 245
Ulota robusta, 31, 160, 247, 276
Ulota rubella, 252, 261
Ulota rufula, 126
Ulota rufula var. *fagicola*, 126
Ulota rufula var. *patagonica*, 118
Ulota savatieri, 163
Ulota scabrida, 92
Ulota schmidii, 280
Ulota scotica, 221
Ulota splendida, 205, 257
Ulota streptodon, 12, 262
Ulota subulata, 186
Ulota subulifolia, 186
Ulota tanganyikae, 7
Ulota ulophylla, 72
Ulota ulophylla subsp. *crispula*, 87
Ulota ulophylla subsp. *eu-ulophylla*, 72
Ulota ulophylla var. *crispula*, 87
Ulota ventricosa, 268, 280
Ulota viridis, 265
Ulota viridis var. *adpressa*, 265
Ulota weymouthii, 72
Ulota yakushimensis, 116, 269
Ulota yunnanensis, 46, 274
Ulotrichum coarctatum, 61
Ulotrichum crispulum, 87
Ulotrichum curvifolium, 92
Ulotrichum drummondii, 103
Ulotrichum hutchinsiae, 138
Ulotrichum phyllanthum, 221

W
Weissia, 3, 34
Weissia americana, 138
Weissia coarctata, 61
Weissia crispa, 71
Weissia crispula, 86
Weissia curvifolia, 92
Weissia drummondii, 103
Weissia intermedia, 145
Weissia maritima, 221
Weissia phyllantha, 221
Weissia ulophylla var. *crispula*, 87
Weissia ulophylla var. *intermedia*, 145
Weissia vittata, 57

Z
Zygodon, 289
Zygodon ventricosus, 280

Appendix. List of All Legal Names in Genus *Ulota*

Only legal names in the Tropicos database are listed here, including recognized ones, synonyms, subspecies, and varieties. The exclamation mark indicates the type of specimens examined in this study.

U. alaskana Cardot & Thér., Proc. Wash. Acad. Sci. 4: 309. 15 f. 4. 1902. Type: U.S.A. Alaska, Glacier Bay, Point Gustavus, 6 Oct. 1899, *F. Coville & T. Kearney 774* (isolectotype, PC! S!); New Metlakatla, 6 Apr. 1899, *W. Trelease 2239* (syntype, PC!); Wrangell, 5 Jun. 1899, *F. Coville & T. Kearney 407* (syntypes, BM! MO! S!).

U. americana Mitt., J. Linn. Soc., Bot. 8: 26. 1864. Type: British N. America upon the rocks called Hell's Gates, *Drummond 153* (holotype, NY).

U. anceps Venturi, Öfvers. Finska Vetensk.-Soc. Förh. 35: 42. 1893. Type: AUSTRALIA. Tasmania: Mt. Wellington, Springs to Ferntree, 7 Mar. 1891, *W. A. Weymouth 900* (holotype, H; isotype, HO).

U. anderssonii (Müll. Hal. ex Ångstr.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877–78: 427. 1880. Type: CHILE. Porte Famine, Feb. 1852, *N. J. Andersson* (not located).

U. angusti-limbata E.B. Bartram, Bryologist 48: 116. 1945. Type: PAPUA NEW GUINEA. Rawlinson Range, alt. 7000–12000 ft., 22 Jul. 1941, *Clemens no. 12445B. 1.* (holotype, FH! isotype, MICH!)

U. angustissima Müll. Hal., Hedwigia 36: 104. 1897. Type: CHILE. Valdivia, 1888, *Dr. H. Hahn* (holotype, G; isotypes, S! NY).

U. aurantiaca Dusén ex Malta, Acta Horti Bot. Univ. Latv. 2: 184, f. 7. 1927. Type: CHILE. Patagonia, 21 Nov. 1895, *P. Dusén 15a* (holotype, S!).

U. barclayi Mitt., J. Linn. Soc., Bot. 8: 26–27. 1865 [1864]. Type: U.S.A. Alaska, Sitka, *Barclay s.n.* (holotype, NY; isotypes, BM! FH!).

U. bellii Malta, Acta Horti Bot. Univ. Latv. 7: 15. ic. 1933. Type: NEW ZEALAND. Lake Harris, Feb. 1895, *W. Bell* (holotype, H! isotype, BM!).

U. bellii var. *longicolla* Malta, Acta Horti Bot. Univ. Latv. 7: 16. ic. 1933. Type: NEW ZEALAND. South Island, Jan. 1902, *R. Brown* (type, BM!).

U. bellissima Besch., Ann. Sci. Nat., Bot., sér. 7, 15: 57. 1892. Type: CHINA. Yunnan, on branches of trees, alt. 3000 m, 5 Aug. 1883, *Delavay 1647* (holotype, FI! isotype, BM! PC! S!).

U. bicolor Brid., Bryol. Univ. 1: 792. 1827. Type citation: “In insulà Terre Neuve arborum cortici adrepens et adeo tenaciter adhaerens ut vix illaesa separari queat, densissime caespitosa habitat. Clar. La Pylaie detector nos illius compotes fecit.” (holotype, B).

U. billbuckii Garilleti, Mazimpaka & F. Lara, Bryologist 115(4): 587. 2012. Type: Chile. Región de Magallanes y de La Antártica Chilena. Provincia Antártica Chilena, Comuna de Cabo de Hornos. Parque Nacional Alberto de Agostini, north-central west of Isla Hoste, ca. 5 km W of the eastern tip of Isla Gordon along SW arm of Beagle Channel in unnamed sound, 55°00′22″ S, 69°12′11″ W, 2 m a.s.l., branches of *Nothofagus antarctica*, 19 Jan. 2012, *R. Garilleti s.n.* (holotype, NY; isotype, VAL).

U. brevicollis (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 164. 1874. Type: Chile. prope urbem Valdivia, 1850, *W. Lechler 527* ex parte (holotype, NY; isotype, S! PC!).

U. breviseta Malta, Acta Horti Bot. Univ. Latv. 7: 9. 1933. Type: New Zealand. Mungatui, Jan. 1888, *W. Bell* (lectotype, H! designated by Fife, 2017); Lake Waikaremoana, 28 Dec. 1932, *Sainsbury* (paratype, BM!).

U. bruchii Hornsch. ex Brid., Bryol. Univ. 1: 794. 1827. Type citation: “Circa Bipontium in arboribus caespitosam clar. Bruch detexit, clar. Funck etiam in monte Pinifero legit et communicavit.” (not located).

U. bruchii var. *marchica* (Warnst.) Paris, Index Bryol. Suppl. 327. 1900. Type: Germany. Neuruppin (Brandenburg), 15 Sep., *C. Warnstorf* (not located).

U. bruchii var. *norvegica* Grönvall, Bidr. Känned. Nord. *Orthotrichum* & *Ulota* 22. 1885. No type information is available for us.

U. bruchii var. *symmetrica* Warnst., Krypt.-Fl. Brandenburg, Laubm. 356. 1904. No type information is available for us.

U. calvescens Carrington, Bryoth. Eur. 11: 520. 1862. Type: Ireland. Tore mountain, May 1861, *Dr. Carrington* (holotype, BM! isotype M! HBG!).

U. camptopoda Kindb., Cat. Canad. Pl., Musci 85. 1892. Type: Canada. Quebec, cemetery W of Hull, Aylmer Road, 26 Apr. 1891, *J. Macoun 582* (lectoype, FH! isolectotype, CANM! FH!).

U. carinata Mitt., J. Proc. Linn. Soc., Bot. 4: 75. 1859. Type: Chile. Chiloe, *Mr. Lobb 35* (holotype, NY; isotype, MICH! BM!).

U. cervina Hoe & H.A. Crum, Bryologist 74 (4): 487. f. 10–13. 1971 [1972]. Type: Hawaiian Islands. Maui, Kipahulu Valley, vicinity of Base Camp no.3, 28 Aug. 1967, abundant as small cushions, more or less exposed, usually on older portions of various stems and branches, ohia (*Metrosideros*) forest, alt. 6375–6400 ft., *W. J. Hoe 1803.0* (holotype, MICH! isotypes, ALTA, BISH, BO, CAN, COLO, DUKE, F, FH, H, MO, NICH, NY, PC, S! UBC, US, Herb.Hoe).

U. chilensis (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 164. 1874. Type: Chile. prope urbem Valdivia, 1850, *W. Lechler 527* (type, NY).

U. coarctata (P. Beauv.) Hammar, Monogr. Orthotrich. Ulot. Suec. 25. 1852. Type: “De l’Amérique septentrionale” comm. *Persoon* (lectotype, G, designated by Vitt, 1970); *Richard* (paralectotype, G).

U. cochleata Venturi, Öfvers. Finska Vetensk.-Soc. Förh. 35: 42. 1893. Type: Australia. Tasmania, Mt. Wellington, Springs to Falls, 2 Mar. 1891, *W. A. Weymouth 898* (holotype, TR; isotype, HO!).

U. connectens (Kindb.) Kindb., Enum. Bryin. Exot., Suppl. 2: 108. 1891. Type: Canada. Ontario, near Ottawa, on cedar trees near the pond in Dow’s swamp, 11 Sep. 1889, *J. Macoun* (syntypes, CANM, NY).

U. crassifolia (Hook. f. & Wilson) Hook. f., Handb. N. Zeal. Fl. 433. 1867. Type: New Zealand. Lord Auckland’s group and Campbell’s Island, on rocks and stones, near highwater mark, *J. D. Hooker* (not located).

U. crenato-erosa (Müll. Hal.) Kindb., Enum. Bryin. Exot. 79. 1888. Type: Clarence Island. Hope Harbour, ad ligna putrida in sylvis, May 1882, *Spegazzini* (not located).

U. crispa (Hedw.) Brid., Muscol. Recent. Suppl. 4: 112. 1819 [1818]. Type: “In saxis, arborum truncis per omnem Europam.” (lectotype, G, designated by Vitt, 1970).

U. crispa subsp. *crispula* (Bruch) Hérib., Mém. Acad. Sci. Clermont-Ferrand 14: 333. 1899. Type: see *U. crispula* Bruch.

U. crispa subsp. *intermedia* (Schimp.) Hérib., Mém. Acad. Sci. Clermont-Ferrand 14: 333. 1899. Type: see *U. intermedia* Schimp.

U. crispa var. *alaskana* (Cardot & Thér.) Grout, Moss Fl. N. Amer. 2: 134. 1935. Type: see *U. alaskana* Cardot & Thér.

U. crispa var. *crispula* (Bruch) Hammar, Monogr. Orthotrich. Ulot. Suec. 24. 1852. Type: see *U. crispula* Bruch.

U. crispa var. *longifolia* (Dixon & Sakurai) Z. Iwats., J. Hattori Bot. Lab. 21: 143. 1959. Type: *U. longifolia* Dixon & Sakurai.

U. crispa var. *microcarpa* Brockm., Arch. Vereins Freunde Naturgesch. Mecklenburg 23: 86. 1870. Type: GERMANY. Im Rabsteinfelder Holze bei Schwerin an Eichen (not located).

U. crispa var. *minor* Brid., Bryol. Univ. 1: 301. 1826. Type: GERMANY. “in Thuringiae sylvis.” (not located).

U. crispa var. *norvegica* (Grönvall) A.J.E. Sm. & M.O. Hill, J. Bryol. 8: 431. 1975. Type: see *U. bruchii* var. *norvegica* Grönvall.

U. crispa var. *propagulifera* J.J. Amann, Fl. Mouss. Suisse 2: 150. 1918. No type information is available for us.

U. crispa var. *subcalvescens* Cardot & Thér., Proc. Wash. Acad. Sci. 4: 310. 1902. Type: U.S.A. Alaska, Baranof Island, 1899, *W. Trelease 2348* (isotype, MO!).

U. crispa var. *typica* Grönvall, Bidr. Känned. Nord. *Orthotrichum* & *Ulota* 22. 1885. No type information is available for us.

U. crispula Bruch, Bryol. Univ. 1: 793. 1827. Type: In arboribus sylvaticis c. Bipontium clar. Bruch detexit; a quo ut et a Funckio amice communicatum habemus. GERMANY. Rheinland-Pfalz, Zweibrücken. ”An Waldbäumen bey Zweybrücken, *Bruch s.n.*” (lectotype, B! proposed by Caparrós *et al.*, 2016)

U. crispula var. *ambigua* Schimp., Syn. Musc. Eur. 258. 1860. Type: ad Fagos Hassiae superioris et prope Jever Oldenburgiae (not located).

U. crispula var. *depexa* De Not., Atti Reale Univ. Genova 1: 289. 1869. Type citation: “Ad fagos in apennino Liguriae orientalis, ad montem *Ariona*, Caldesi, ad Betulas prope *Cavergna* in pago Ticinensi, Franzoni; ad fagos in monte *Monterone* et varietatem ß. ad truncum fraxini in valle *Intrasca*, ad Verbanum ipse legi.” (not located).

U. crispula var. *dolosa* Renauld & Cardot, Bot. Gaz. 22: 51. 1896. Type: U.S.A. District of Columbia, Tenallytown, 1892, *J. M. Holzinger* (type, FH!).

U. curvifolia (Wahlenb.) Sw., Utkast Sv. Fl. (ed. 3) 546. 1816. Type: NORWAY. “in saxorum lateribus umbrosis subirrigatis per partem sylvaticam Lapponiarum et inferalpinam Nordlandiae rarius”, 17 Aug. 1807, *s.coll.* (holotype, S!).

U. darwinii Mitt., J. Proc. Linn. Soc., Bot. 4: 77. 1859. Type: ARGENTINA. Terra del Fuego, 1833, *C. Darwin* (holotype, NY; isotype, BM, PC!).

U. delicata Q.H. Wang & Y. Jia, Bryologist 115(3): 420. 2012. Type: CHINA. Fujian, Mt. Wuyi, Sangang, roadsides to Xianglufeng, on the pine, alt. 1200 m, 20 Apr. 1955, *bryophyte training class 933-d* (holotype, PE!).

U. dixonii Malta, Acta Horti Bot. Univ. Latv. 7: 19. 1933. Type: AUSTRALIA. Tasmania, South part of the Island, Hartz Mountains, on limbs of tree, alt. 3000 ft., 7 Jan. 1908, *W. A. Weymouth 2299* (holotype, H! isotypes, BM! HO!).

U. dixonii var. *novae-seelandiae* Sainsbury, Rev. Bryol. Lichénol. 18: 112. 1949. Type: NEW ZEALAND. North Island, Taranaki, Mt. Egmont, Fantham’s Peak track, on bark of subalpine scrub, at ca. 4000 ft, 16 Jan. 1945, *G. O. K. Sainsbury 10443* (not located).

U. drummondii (Hook. & Grev.) Brid., Bryol. Univ. 1: 299. 1826. Type: U.K. Scotland, near Forfar, Glen Fallach, 1823, *T. Drummond 60* (lectotype, E!)

U. drummondii var. *anceps* I. Hagen, Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1907(13): 22. 1908. Type: no type information in the protologue.

U. ecklonii (Hornsch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 163. 1874. Type: SOUTH AFRICA. Cape Tafelberg, *Ecklon s.n.* (holotype, BM! isotype, S! PRE!).

U. eremitensis Mitt., J. Proc. Linn. Soc., Bot. 4: 76. 1859. Type: CHILE. Tierra del Fuego, "Hermite Island, Cape Horn", *J. D. Hooker s.n.* (holotype, NY).

U. eurystoma Nog., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 3: 213. 18 f. 1–10. 1939. Type: JAPAN. Honshu, Mt. Hirakura, 29 Mar. 1938, *R. Toyama 2650* (isotype, KYO!).

U. fernandeziana Malta, Acta Horti Bot. Univ. Latv. 2: 202. f. 20. 1927. Type: CHILE. Juan Fernandez, Masafuera, Cordon de Borril, an Drimys, 1 Mar. 1917, *C. et I. Skottsberg sub n.165* (holotype, H! isotype, S!).

U. fuegiana Mitt., J. Proc. Linn. Soc., Bot. 4: 76. 1859. Type: CHILE. Tierra del Fuego, "Hermite island, Cape Horn", 1839–1843, *J. D. Hooker 141b* (holotype, NY; isotype, BM! E! PC!).

U. fuegiana subsp. *darwinii* (Mitt.) Malta, Acta Horti Bot. Univ. Latv. 2: 188. 1927. Type: see *U. darwinii* Mitt.

U. fuegiana var. *crispata* Malta, Acta Horti Bot. Univ. Latv. 2: 202. 1927. Type: CHILE. Valdivia, 1888, *H. Hahn* (holotype, H! isotype, S!).

U. fulva Brid., Bryol. Univ. 1: 301. 1826. Type: RÉUNION, 'in insulae Borboniae arboribus caespitose habitat, Bory St. Vincent detexit.' (lectotype, PC! designated by Wang and Jia, 2012b; isolectotype, BM!)

U. funstonii Grout, Moss Fl. N. Amer. 2: 137. pl. 57: A. 1935. Type: U.S.A. Alaska, vicinity of Yakutat Bay, *Funston 158* (holotype, US).

U. germana (Mont.) Mitt., J. Proc. Linn. Soc., Bot. 4: 76. 1859. Type: CHILE. "in corticibus arborum reipublicae chilensis a cl. *Claude Gay.* lectum" (lectotype, PC! designated by Garilleti *et al.*, 2020; isolectotypes, BM! PC!).

U. germana var. *breviseta* Malta, Acta Horti Bot. Univ. Latv. 2: 202. 1927. Type: CHILE. Río Aysen, Jan. 1897, *P. Dusén 434* (lectotype, H, designated by Garilleti *et al.*, 2020; isolectotype, S).

U. gigantospora F. Lara, Caparrós & Garilleti, J. Bryol. 33(3): 214. 2011. Type: CHINA. Sichuan, Jiulong County, mountain tributary of Wuxuhai-Jiulong valley below pass above Shandaoqiao village, SW of Jiulong, 28°58′6.6″ N, 101°24′1.9″ E, alt. ca. 4200 m; mossy *Abies*/ *Rhododendron* forest along small stream; on *Abies* trunk, 17 Sep. 2010, *D. G. Long 40246* (holotype, E!).

U. glabella Mitt., J. Proc. Linn. Soc., Bot. 4: 76. 1859. Type: CHILE. Tierra del Fuego, "Hermite island, Cape Horn", 1839–1843, *J. D. Hooker 141a* (holotype, NY; isotype, BM, E, PC).

U. gymnomitria Müll. Hal., Hedwigia 36: 104. 1897. Type: ARGENTINA. Patagonia, in Museo de La Plata, 1882, *E. P. Moreno* (holotype, NY).

U. gymnostoma S.L. Guo, Enroth & Virtanen, Ann. Bot. Fenn. 41: 459. 2004. Type: CHINA. Hunan, Changsha Area, Liu Yang Co., Daweishan National Forest Park, along road from Lu-Yuan hotel towards Tian-Xing Hu, 25°25′ N, 114°07′30″ E, ca. 1400 m., on trunk of *Prunus persica*, 20 Sep. 2000, *Virtanan 62091* (holotype, H!).

U. hamata Dusén, Rep. Princeton Univ. Exp. Patagonia, Botany 8(3): 82. 11, t. 9. f. 4. 1903. Type: CHILE. "Patagonia australis in truncis arborum", 1896–1897, *J. B. Hatcher* (holotype, S; isotype, PC!).

U. hattorii Z. Iwats., J. Hattori Bot. Lab. 32: 280. f. 7. 1969. Type: MALAYSIA [BORNEO], Sabah, Mt. Kinabalu, on branches and trunks of trees, on granodiorite slope below Sayat Sayat, alt. 3350–3700 m, 20 May 1963, *Z. Iwatsuki 949* (holotype, NICH!).

U. hutchinsiae (Sm.) Hammar, Monogr. Orthotrich. Ulot. Suec. 27. 1852. Type: U.K. England, near Bantry*, Hutchins* (not located).

U. hutchinsiae var. *rufescens* (E. Britton) Dixon, Stud. Handb. Brit. Mosses 244. 1896. Type citation: "Summit of White Top, on trees in dense woods of *Picea Mariana* and *rubra*, mixed with *Dicranum longifolium*, *Zygodon viridissimus*, *W. ulophylla* and *Frullania Asa-Grayana*, alt. 5678 ft." (not located).

U. immarginata Cardot, Bull. Herb. Boissier, sér. 2, 5: 1004. 1905. Type: ARGENTINA. "Terre-de-Feu: Ushuaia, ad trunc. *Nothofagi antarcticae*, 25 Sep. 1902, *C. Skottsberg 91*" (holotype, PC! isotype, S!).

U. incana (Müll. Hal.) Kindb., Enum. Bryin. Exot. 79. 1888. Type: CHILE. Fuegia, Voces Bay in Brunsvich Peninsula ad fretum Magellanicum, in sylvis ad ramos *Drymidis Winleri*, May 1882, *Spegazzini* (lectotype, H).

U. inclinata (Müll. Hal.) Kindb., Enum. Bryin. Exot. 79. 1888. Type: "Fuegia occidentalis, Basket Island, Desolation Bay, inter *Syntrichiam*, Junio 1882" (not located); "Uhsuvaia, Beagle Channel, ad ligna putrida in sylvis, Majo 1882, *Spegazzini*" (not located).

U. intermedia Schimp., Syn. Musc. Eur. (ed. 2) 305. 1876. Type: "in Hassia superior ad Fagos male evolutas (BRUCH), prope *Jever* Oldenburgiae, ipse copiose legi ad arborum, praeprimis Fraxini et Aceris truncus in valle Scotiae *Loch Lomond*." GERMANY. Hesse, Marburg-Biedenkopf, "Ludwigshütte. Jul. Aug. 41. Bruch m. Nov. 41" (lectotype, BM, designated by Caparrós *et al.*, 2016)

U. japonica (Sull. & Lesq.) Mitt., Trans. Linn. Soc. London, Bot. 3: 162. 1891. Type: JAPAN. Hokkaido, Hakodadi, collected on trees shaded Hill sides during Com. Rogers N. Pacific Expl. Exp., Aug. 1859, *Charles Wright* (holotype, FH!).

U. japonica var. *stenocarpa* Cardot, Bull. Herb. Boissier, sér. 2, 8: 336. 1908. Type: JAPAN. Kuroishi, *Faurie 11* (not located); Aomori, *Faurie 2643* (not located).

U. larrainii Garilleti, Mazimpaka & F. Lara, Phytotaxa 217(2): 133. 2015. Type: CHILE. Prov. Capitán Prat: Caleta Tortel, comienzo de "ruta turística", en tundras de *Donatia*, *Astelia* y *Lepidothamnus fonkii*, 47°47′32″ S, 73°31′48″ W, alt. ca. 90 m, epífito en *Nothofagus dombeyi*, 20 Ene[ro] 2007, *J. Larraín 26884A, con R. Vargas* (holotype, VAL-Briof; isotype, CONC).

U. lateralis (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877–78: 427. 1880. Type: AUSTRALIA. ad Hume River etc (not located).

U. laticiliata Malta, Acta Horti Bot. Univ. Latv. 7: 11. 1933. Type: AUSTRALIA. Tasmania, S. E. Coast, Recherche Bay, "Moss Glen", near Ramsgate, on apple trees, at sea level, 17 Jan. 1911, *W. A. Weymouth 2487* (lectotype, H! designated by Ramsay, 2006; isolectotype, HO!); Tasmania, Mt. Wellington, 6 Mar. 1891, *W. A. Weymouth 227* (paralectotype, H; isoparalectotype, HO).

U. latisegmenta Q.H. Wang & Y. Jia, Bryologist 115(3): 429. 2012. Type: CHINA. Sichuan Prov., Emei mountain, near Jinding, on trunk, 25 Aug. 1942, *P.-C. Chen 5596* (holotype, PE!).

U. lativentrosa Müll. Hal. ex Malta, Acta Horti Bot. Univ. Latv. 2: 194. fi. 14. 1927. Type: CHILE. Valdivia, Anden von Villarica, 1897, *D. Neger* (holotype, B, absent; isotype, M!).

U. leiothecia (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 161. 1874. Type: CHILE. Sandy Point, *W. Lechler 1020* (lectotype, PC! designated here; isolectotype, S!).

U. lobbiana Mitt., J. Proc. Linn. Soc., Bot. 3: 75. 1859. Type: CHILE. Patagonia, *Mr. Lobb 35b* (holotype, NY; isotype, BM! MICH!).

U. longifolia Dixon & Sakurai, Bot. Mag. (Tokyo) 49: 140. 1935. Type: JAPAN. Hondo, Prov. Sagami, Hakone-pass, Aug. 1910, *K. Sakurai 193* (not located).

U. ludwigii (Brid.) Brid., Muscol. Recent. Suppl. 4: 112. 1819 [1818]. Type: "In Lufatià et circa Lipfiam ad arbores Ludwigius detexit et nobiscum communicavit"., 1811, *Ludwig* (type, B!); 1812, *Ludwig* (type, B!).

U. lutea (Hook. f. & Wilson) Mitt., J. Proc. Linn. Soc., Bot. 4: 77. 1859. Type: AUSTRALIA. Tasmania, Western Mountains, rivulet behind Cumming's Head, on trees, Archer (lectotype, NY! designated by Wang and Jia, 2012b; isolectotype, HO!).

U. luteola (Hook. f. & Wilson) Wijk & Margad., Taxon 10: 26. 1961. Type: CHILE. Tierra del Fuego, "Hermite Island, Cape Horn.", 1839–1843, *J. D. Hooker 141b* (holotype, NY; isotype, H!).

U. macrocalycina Mitt., J. Proc. Linn. Soc., Bot. 4: 75–76. 1859. Type: CHILE. Straits of Magellan, on trunks of trees, Port Famine, Sep. 1851, *Dr. Lyall* (holotype, NY; isotype, BM! PC!).

U. macrocarpa Broth., Symb. Sin. 4: 70. 1929. Type: CHINA. Hunan Prov., Prope urbem Wukang, in silva frondosa elata umbrosa montis Yün-schan, ad arbores, alt. 1200–1300 m, 8 Aug. 1917, *Dr. Heinr. Frh. v. Handel-Mazzetti (Diar. Nr. 2206)*, (lectotype, H! designated by Guo *et al.*, 2004); Sichuan Prov., Huili, Lungdschu-schan (Mt. Longzhou), "an Bambushalmen", 3000–3675m, 26 Mar. 1914, *Dr. Heinr. Frh. v. Handel-Mazzetti 820* (isoparatype, S!).

U. macrodontia Dixon & Malta, Acta Horti Bot. Univ. Latv. 2: 204. ic. 1927. Type: CHILE. Río Aysén, in ramulis, 14 Jan. 1897, *Dusén 434* (lectotype, S! designated by Wang and Jia, 2016; isolectotype, H!); 4 Feb. 1897, *Dusén 516* (paratype, S!); 1897, *Dusén s.n.* (paratype, S!).

U. macrospora Baur & Warnst., Hedwigia 32: 259. 1893. Type: GERMANY. Harwood at Achern, on spruce stems, 20 Jul. 1891, *W. Baur* (not located); on spruce trees in the forest near Cologne, three hours from Karlsruhe, 22 Jul. 1891, *W. Baur* (not located).

U. magellanica (Mont.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 164. 1874. Type: CHILE. Magellan, Port Famine, *M. Jaequinot* (lectotype, PC! designated by Wang and Jia, 2016).

U. maltiana Garilleti & F. Lara, Bryologist 123(2): 165. 2020. Type: CHILE. Región Aysén Del General Carlos Ibáñez Del Campo: Provincia de Aysén, Comuna de Cisnes, Parque Nacional Queulat, entrance to Ventisquero Colgante, 44°28′17″ S, 72°33′34″ W, 40 m, moss forest of *Nothofagus betuloides*, on *N. dombeyi*, 28 Dec. 2016, *R. Garilleti 2016-231a & F. Lara* (holotype, VAL-BRIOF 11822; isotypes, CONC, BM, MAUAM).

U. mandonii (Schimp. ex Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 163. 1874. Type: BRAZIL. Nova-Granada, Paramo Coachi 3000 m ad ramos, *A. Lindig* (not located); PORTUGAL. insula Madeira, *Mandon* (not located).

U. marchica Warnst., Hedwigia 28: 372. 1889. Type citation: GERMANY. "Neuruppin (Brandenburg): An Erlenstämmen am Tornow-See unweit des Flössergrundes in Gesellschaft von *U. bruchii*, *crispa* und *crispula* am 15 Sept. d. J. von mir mit reifen Früchten gesammelt." (not located).

U. marchica subsp. *macrospora* (Baur & Warnst.) Broth., Nat. Pflanzenfam. I(3): 1201. 1909. Type: see *U. macrospora* Baur & Warnst.

U. marginata (Ångstr.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877–78: 427. 1880. Type: CHILE. Pork Famine, *J. Andressaw* (holotype, S!).

U. maritima Müll. Hal. & Kindb., Cat. Canad. Pl., Musci 84. 1892. Type: MIQUELON ISLAND. *Delamare* (syntype, PC! S!); CANADA. British Columbia, Hastings, 11 Apr. 1889, *Macoun* (syntype, NY); U.S.A. Alaska, Unalaska Island and Kodiak Island, 22 Sept. 1891, *Macoun* (syntype, CANM, S!).

U. megalospora Venturi, Bot. Centralbl. 44(12): 389. 1890. Type: U.S.A. Washington, Cascaden, Rigi prope Clealum Lake, *Röll*, 1889 (lectotypes, FH! designated by Vitt, 1970; isolectotype, NY!).

U. membranata Malta, Acta Horti Bot. Univ. Latv. 7: 18. 3. 1933. Type: AUSTRALIA. Tasmania, West coast, Comet-Dundas Road, on wood, 17 Oct. 1893, *W. A. Weymouth 1652* (holotype, H! isotypes, HO! TR).

U. morrisonensis Horik. & Nog., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 3: 37, 1. 1937. Type: CHINA. Taiwan, Tainan, Mt. Yushan (Japanese name: Mt. Niitaka), alt. ca. 3300 m, 19 Aug. 1932, *A. Noguchi 5985* (holotype, HIRO; isotype, NICH!).

U. nicholsonii Culm., Rev. Bryol. 53: 21. 1926. Type: IRELAND. West Mayo, Achill Island, *Croaghaum, Rocks,* 20 Jul. 1925, *I. B. Duncan, H. H. Knight and W. E. Nicholson* (type, NY).

U. nigricans Brid., Bryol. Univ. 1: 792. 1827. Type: CANADA. Terre Nueve, 1825, *LaPylaie* (holotype, B!).

U. nigrita (Bruch & Schimp.) Schimp., Coroll. Bryol. Eur. 41. 1856. Type citation: "Ad rupes in loco "Rofflen" dicto prope Andeer Montis Splügen Helvetiae. Rarissima stirps, ab amico ALEX. BRAUN anno 1825 detecta, nobiscum humaniter communicata." (not located).

U. nipponensis Besch., Ann. Sci. Nat., Bot., sér. 7, 17: 339. 1893. Type: JAPAN. Kuroishi, 25 Apr. 1887, *Faurie 11b* (lectotype, PC! designated here; isolectotypes, BM! KYO! S!); Sambongi, 6 Jun. 1886, *Faurie 554* (paralectotype, PC!).

U. nothofagi Cardot, Bull. Herb. Boissier, sér. 2, 5: 1005. 1905. Type: ARGENTINA. Terre-de-Feu, Ushuaia, troncs de *Nothofagus antartica* et *betuloides*, 25 Sep. 1902, *C. Skottsberg 85* (lectotype, PC!), *C. Skottsberg 84* (paratypes, H! PC! S!), *C. Skottsberg 86* (paratype, PC!).

U. novae-seelandiae Sainsbury, Bull. Roy. Soc. New Zealand 5: 223. 1955. Type: NEW ZEALAND. North Island, Taranaki, Mt. Egmont, Fantham's Peak Track, on bark of subalpine scrub, at ca. 4000 ft, 16 Jan. 1945, *G. O. K. Sainsbury 10443* (holotype, WELT!).

U. novo-guinensis E.B. Bartram, Brittonia 11: 91. 1959. Type: PAPUA NEW GUINEA. Eastern Highlands, Chimbu sub-district, above Lake Punda, e slope Mt. Wilhelm, on branches of small tree, alt. ca. 3950 m, 24 Jul. 1956, *R. D. Hoogland & R. Pullen 5765* (holotype, FH! isotype, L!).

U. obtusiuscula Müll. Hal. & Kindb., Cat. Canad. Pl., Musci 82. 1892. Type: CANADA. British Columbia, on small maple trees in thickets along the Coquihalla River near New Westminster Junction, 26 Apr. 1889, *J. Macoun* (isolectoypes, NY! designated here; isolectotype, BM! FH! MO! NY!); Vancouver Island, Fort Rupert, 1885, *Dawson* (paralectotypes, NY! CANM).

U. orientalis Fedosov & Ignatova, Novosti Sist. Nizsh. Rast. 52(1): 143, P. I, II, Figure 1. 2018. Type: RUSSIA. Khabarovsk Territory, 26 Aug. 2013, *Ignatov & Ignatova 13-1218* (holotype, MHA; isotype, MW).

U. pacifica Fedosov & Ignatova, Novosti Sist. Nizsh. Rast. 52(1): 145, Pl. III, IV, Figure 1. 2018. Type: RUSSIA. Sakhalin Region, Iturup Island, 11 Sep. 2015, *Fedosov 15-2-154* (holotype, MW; isotype, MHA).

U. paivana Schimp., Flora 69: 347. 1886. *invalid, cited as synonym.* Type: PORTUGAL. Madeira, Boroaca, 16 Jan. 1866, *A. Paiva s.n.* (holotype, BM)

U. panchengiana Q.H. Wang & Y. Jia, Cryptog., Bryol. 39(4): 468, 1–28. 2018. Type: CHINA. Sichuan Prov., Wenchuan Co., Weizhouzhen, Qipangoucun, Mt. Guangguangshan, 31°24′13″ N, 103°35′55″ E, alt. 2400 m, on tree trunk, 27 Aug. 2002, *Y. Jia 06671b* (holotype, PE! isotype, MO!).

U. perbreviseta Dixon & Sakurai, Bot. Mag. (Tokyo) 49: 139. 1935. Type: JAPAN. Hondo, Ohmi Prov., Mt. Ibuki, an Sträuchern, May 1923, *K. Sakurai 1070* (holotype, BM!).

U. perichaetialis (Sainsbury) Goffinet, Bryol. Twenty-first Cent. 153. 1998. Type: NEW ZEALAND. North Island, Taranaki, Mt. Egmont, Fantham's Peak Track, on bark of subalpine scrub, alt. 1219 m, 16 Jan. 1945, *G. O. K. Sainsbury 6476* (lectotype, WELT! designated by Fife, 2017).

U. phyllantha Brid., Muscol. Recent. Suppl. 4: 113. 1819 [1818]. Type: DENMARK. "E Danice maritimus. Ludwigius. 1811" (holotype, B!).

U. phyllantha var. stricta W.E. Nicholson, J. Bot. 38: 134. 1900. Type: U.K. Scotland, rocks by the sea, on the Island of Stroma, in the Pentland Frith, *Dr. P. B. Mason* (type, BM!).

U. phyllanthoides (Müll. Hal.) Kindb., Enum. Bryin. Exot., Suppl. 1 96. 1889. Type: Gazelle-Expedition, *Dr. Naumann* (not located).

U. pilifera Nees, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19, Suppl. 1: 477. 1843. Type information is not available for us.

U. plicata (P. Beauv.) Brid., Muscol. Recent. Suppl. 4: 113. 1819 [1818]. Type: no type information in the protologue.

U. pusilla Malta, Acta Horti Bot. Univ. Latv. 2: 193. f. 13. 1927. Type: CHILE. Tierra del Fuego, Almirantazgo, 1908, *Halle & Skottsberg 460a* (holotype, H! isotype, PC!).

U. pycnophylla Dusén ex Malta, Acta Horti Bot. Univ. Latv. 2: 183. f. 6. 1927. Type: CHILE. Cordillera de la Costa, Angol, an Stämmen, elev. 700 m, 4 Nov. 1896, *P. Dusén 346b* (holotype, S!).

U. pygmaeothecia (Müll. Hal.) Kindb., Enum. Bryin. Exot. 79. 1888. Type: CHILE. Fuegia, ad ramos *Maytheni magellanicae* montls Darwin 1882, *Spegazzini* (lectotype, H! designated by Wang and Jia, 2016; isolectotype, PC!).

U. rehmannii Jur., Verh. Zool.-Bot. Ges. Wien 14: 191. 1864. Type: POLAND. On trees in subalpine forests of Tatragebirge near Zakopane, 1862, *A. Rehmann s.n.* (holotype, M! isotype, BP!).

U. rehmannii subsp. *macrospora* (Baur & Warnst.) Podp., Consp. Musc. Eur. 459. 1954. Type: see *U. macrospora* Baur & Warnst.

U. reptans Mitt., Trans. Linn. Soc. London, Bot. 3: 161. 1891. Type: JAPAN. Fujisan, May 1887, *J. Bisset s.n.* (holotype, NY; isotypes, E! NICH! PC!).

U. rhytiore (B.H. Allen) F. Lara, Garilleti, Albertos & Mazimpaka, Bryologist 111(2): 326. 2008. Type: EL SALVADOR. Chalatenango, Mun. Ignacio, Cantón Río Chiquito, Cerro Pital, finca de los Sres. Portillo, cima de Cerro Pital, elev. 2730 m, 14°23′ N, 89°08′ W, exposed mountain top, disturbed low mossy forest, 21 Nov. 1993, *Sipman 37626A* (holotype, NY!).

U. robusta Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 49. 1859. Type: INDIA. Sikkim. Himalaya orient. reg. temp., *J. D. Hooker no.216* (lectotype, BM! designated by Guo *et al.*, 2010; isolectotype, NY), *219* (paralectotypes, NY, BM), *244* (paralectotypes, NY, BM).

U. rubella E.B. Bartram, Lloydia 5: 269. 26. 1942. Type: PAPUA NEW GUINEA. E slope Mt. Wilhelm, subalpine forest, epiphyte, alt. ca. 3800 m, *L. J. Brass & E. Myer-Drees 10374* (holotype, FH! isotypes, L! MICH!).

U. rufescens (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 163. 1874. Type: BRAZIL. Nova-Granada, Bogota los Laches ad arbores, *A. Lindig* (not located).

U. rufula (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872–73: 164. 1874. Type: CHILE. prope urbem Valdivia, 1850, *W. Lechler 527*, ex parte (isotypes, PC! S!).

U. rufula var. *fagicola* Dusén ex Malta, Acta Horti Bot. Univ. Latv. 2: 200. f. 19: a–c. 1927. Type: CHILE. in monte "Cordillera de la Costa" supra Angol app., in truncis arborm, 4 Nov. 1896, *P. Dusén 346a* (holotype, H! isotype, S!).

U. rufula var. *patagonica* Malta, Acta Horti Bot. Univ. Latv. 2: 200. f. 19: d–g. 1927. Type: CHILE. "Río Aysen, in ramulis.", Jan. 1897, *P. Dusén 516* (holotype, H! isotype, PC!).

U. savatieri Besch., Bull. Soc. Bot. France 32: LXII. 1885. Type: CHILE. Patagonie occidentale, Wellington island, Port Edén, 24 Feb. 1877, *Dr. Savatier* (holotype, PC! isotype, BM!).

U. scabrida Kindb., Cat. Canad. Pl., Musci 83. 1892. Type: CANADA. British Columbia, Rocky Mountains, abundant on immense boulders between Cathedral Mountain and Mount Stephen three miles below Hector, 29 Jul. 1885, *J. Macoun* (syntypes, PC! S!); also in the same place and on boulders by the torrent at Hector, Aug. 1890, *J. Macoun* (syntypes, CANM! MO! PC! S!).

U. schmidii (Müll. Hal.) Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 49. 1859. Type: INDIA. Mt. Nilghiri, *Schimds* (lectotype, H!).

U. scotica Stirt., Ann. Scott. Nat. Hist. 14(54): 106. 1905. Type: U.K. Scotland, near Arisaig, on branches of trees (not located).

U. splendida E.B. Bartram, Lloydia 5: 269. 27. 1942. Type: PAPUA NEW GUINEA. Mt. Wilhemina, abundant as an epiphyte in subalpine forest, 2 km E of Wilhemina-top, alt. 3800 m, Sep. 1938, *L. J. Brass & E. Myer-Drees 10137* (holotype, FH! isotypes, BM! L! MICH!).

U. streptodon Garilleti, Mazimpaka & F. Lara, Bryologist 115(4): 594. 2012. Type: CHILE. Región de Magallanes Y de La Antártica Chilena. Provincia Antártica Chilena. Comuna de Cabo de Hornos. Parque Nacional Alberto de Agostini, south-central coast of Isla Gordon, Caleta Caracoles, NW of Estero Fouqué along SW arm of Beagle Channel, 55°01′57″ S, 69°36′41″ W, 5 m a.s.l., patches of tundra and disperse small areas of shrubby *Nothofagus betuloides*, horizontal branches of *Nothofagus betuloides* close to the shoreline, 20 Jan. 2012, *R. Garilleti s.n.* (holotype, NY; isotype, VAL).

U. subulata Müll. Hal. & Kindb., Cat. Canad. Pl., Musci 82. 1892. Type: CANADA. British Columbia, near New Westminster Junction, along the Coquhilla River, Black's Farm, on small trees in thickets, 26 Apr. 1889, *J. Macoun* (type, S!).

U. subulifolia Müll. Hal. & Kindb., Cat. Canad. Pl., Musci 82. 1892. Type: CANADA. British Columbia, near New Westminster Junction, Black's Farm, along the Coquhilla River, on small trees in thickets, 26 Apr. 1889, *J. Macoun* (type, NY).

U. tanganyikae P. de la Varde, Ark. Bot., n.s. 3: 174. f. 25. 1955. Type: TANZANIA. Kilimanjaro, saddle between Kibo and Mawenzi, western slope of Mawenzi, on a shaded rock, alt.4530–4800 m, 19 Jun. 1948, *Olov Hedberg 1273a* (holotype, PC!).

U. ulophylla Broth., Nat. Pflanzenfam. I(3): 473. 1902. Type citation: "an Waldbäumen, besonders an Nadelhölzern, durch die Ebene und Bergregion von Europa fast überall verbreitet, auf den kanarischen Inseln, im Kaukasus, in Amur und auf Sachalin, in Nordamerika ziemlich verbreitet." (not located)

U. ulophylla subsp. *crispula* (Bruch) Giacom., Ist. Bot. Reale Univ. Reale Lab. Crittog. Pavia, Atti 4: 249. 1947. Type: see *U. crispula* Bruch.

U. ulophylla var. *crispula* (Bruch) Weim., Förteckn. Skand. Växt., Moss. (ed. 2) 40. 1937. Type: see *U. crispula* Bruch.

U. ulophylla var. *intermedia* (Schimp.) Jansen & Wacht., Ned. Kruidk. Arch. 53: 215. 1943. Type: see *U. intermedia* Schimp.

U. ventricosa (Müll. Hal.) Malta, Acta Horti Bot. Univ. Latv. 2: 180. 1927. Type: CHILE. *Philippi* (not located); Punta Arenas, 21 Dec. 1895, *P. Dusén* (not located).

U. viridis Venturi, Öfvers. Finska Vetensk.-Soc. Förh. 35: 43. 1893. Type: AUSTRALIA. Tasmania, Mt. Wellington, near the springs, on wood, 15 Oct. 1890, *W. A. Weymouth 901* (holotype, TR; isotypes, H! HO!).

U. viridis var. *adpressa* Malta, Acta Horti Bot. Univ. Latv. 7: 22. 1933. Type: NEW ZEALAND. Otago, Mt. Bonpland, on stems of Beech, Jan. 1890, *W. Bell* (lectotype, H, designated by Fife, 2017; isolectotype, CHR).

U. viridis var. *dixonii* (Malta) H.P. Ramsay, Fl. Australia 51: 411. 2006. Type: see *U. dixonii* Malta.

U. vittata Mitt., J. Proc. Linn. Soc., Bot. 8: 3. 1864. Type: PORTUGAL. Madeira, on trees on the mountains, *J. Y. Johnson* (holotype, NY).

U. weymouthii Venturi, Pap. & Proc. Roy. Soc. Tasmania 1912: 114. 1913. Type: AUSTRALIA. Tasmania, Mt. Wellington (not located).

U. yakushimensis Z. Iwats., J. Hattori Bot. Lab. 21: 153. 7f. 1g. 1959. Type: JAPAN. Kagoshima Pref., Island Yakushima, between Kosugidani and Hananoego, 10 Apr. 1950, *H. Hasegawa, M. Fukuhara & Fukui 8343* (holotype, NICH! isotype, NUM!).

U. yunnanensis F. Lara, Caparrós & Garilleti, J. Bryol. 33(3): 211. 2011. Type: CHINA. Yunnan Prov., Zhongdian (Shangrila) Co., N slope of Xiao Xue Shan (Little Snow Mountain), N of Geza, 28°19′38″ N, 99°45′39″ E, alt. 3845 m, *Abies-Rhododendron* forest, on *Quercus*, 28 May 1993, *D. G. Long 23775* (holotype, E! isotypes, PE, MO and herbarium at Universidad Autonoma de Madrid).